

Chapter 4. SEED PRODUCTION IN *CASTANOSPERMUM AUSTRALE*

4.1 INTRODUCTION

Plant species vary in the frequency and synchrony of flowering and in the level of reproductive effort. Strategies vary from regular, annual flowering and fruiting, with low levels of variation in fruit crop size and high individual participation in the flowering event, to asynchronous flowering between individuals, to species which only produce significant flowering and fruiting events every few years. At the extreme, some species may mast fruit, that is the population of trees in an area are synchronized on a supra-annual schedule, so that there is high participation in the event and an individual tree is likely to be fruiting in the same year as its conspecifics (Janzen 1978). This is often also associated with large crop sizes relative to non-mast years. Mast fruiting occurs among many temperate trees such as beech, oak and conifers (Silvertown 1980, Sork 1993). Such fruiting may be a strategy to satiate seed predators (Janzen 1971, 1978), to increase the success of wind pollination, or as a result of synchronised flowering in response to environmental cues or the need to attract pollinators (Kelly 1994).

In tropical systems, fruiting phenologies may be influenced more by rates of fruit maturation and life history strategies, than by environmental cues (Primack 1987, Kinnaird 1992). Physiological factors such as drought stress and the onset of the rainy season may control flowering response, but may not be the driving force themselves (Auspurger 1981, Primack 1987). Rather, the timing of flowering and fruiting is influenced by the need for effective cross pollination between individuals in the population, the concomittant need to attract pollinators, and the need to attract fruit dispersers and satiate seed predators (Primack 1987). The timing of seed release may also be influenced by the best time for a seed to germinate, especially for species which lack seed dormancy or occur in tropical habitats with a pronounced dry season (Primack 1987). Based on a survey of fruiting phenology on Barro Colorado Island, Foster (1982) concluded that fruitfall appears to be a compromise between the desirability of seeds germinating fairly early in the rainy season, and the desirability of flowering early in the rainy season, when pollinators are presumably most abundant. There were very few species which neither flowered nor germinated seeds early in the rainy season.

Seed size may also be influenced by life history strategies such as germination requirements, and by the need to attract fruit dispersers and satiate seed predators. However, there is an evolutionary trade off between seed size and seed number. Large seeds are expensive to

produce for the maternal plant. If a plant produces large seeds, it will tend to produce fewer seeds per fruit, and fewer fruits per plant (Primack 1987). Large fruits tend to have an extended period of fruit maturation (Primack 1987) (although this is not directly related to fruit size (Foster 1982)), during which seeds are prone to pre-dispersal seed predation (e.g. Janzen 1978). On the other hand, seed size and subsequent seedling size is important in determining the success of seedling establishment. Large seeds have a greater chance of seedling success (but see Winn 1988). In tropical moist habitats, large seeds are hypothesized to have a range of advantages for germination, seedling size, and survival in high predation, low light conditions (Foster 1986). There is a tendency for species which establish in the shade to have larger seeds (Foster & Janson 1985), and for plants in stable shady moist habitats to have larger seeds than plants in sunny, disturbed and dry habitats (Baker 1972, Salisbury 1942). Large fruits offer a reward to potential dispersers, thereby increasing the chance that a seed will be dispersed beyond the region of high predation near the parent plant, and to a suitable site for germination (Howe & Smallwood 1982). Large seeds tend to have large specialised dispersers, generally vertebrates (Primack 1987). Tropical moist habitats have a large proportion of fleshy-fruited (Willson *et al.* 1989) and large-fruited species. In Asia and the neotropics, these offer rewards for the large vertebrate dispersal vectors.

In this chapter, data on seed, pod and fruit crop size of *C. australe* are presented, to investigate timing and quantity of fruit production and the availability of this resource for predators.

4.2 SPECIES DESCRIPTION

Black Bean (*Castanospermum australe* Cunn. & C. Fraser ex Hook.) is a large tree up to 35m height (in N.S.W., Floyd 1989) and 140cm girth. It occurs in subtropical and tropical rainforest, and its distribution ranges from the Orara and Bellinger Rivers, northeastern New South Wales, to Iron Range, Cape York Peninsula in northern Queensland, as well as New Caledonia and New Hebrides (Floyd 1989). Within Australia, its distribution ranges from latitude 12.5 - 29°S, and altitude 50-750m (Figure 3.7); mean rainfall across the distribution varies from less than 1000 mm to 3800 mm (Boland *et al.* 1984). In New South Wales, *C. australe* occurs along the banks of streams in riverine rainforest, and in rainforest on level terraces on mountain sides (Floyd 1989).

In New South Wales, *C. australe* is relatively abundant in the *Castanospermum-Dysoxylum muelleri* suballiance within the *Argyrodendron trifoliolatum* subtropical rainforest alliance,

and the *Castanospermum-Waterhousia floribunda* dry rainforest (Floyd 1989). The *Castanospermum-Dysoxylum* suballiance occurs on the Alstonville plateau, Border Ranges terraces and on alluvial floodplains, including the Tweed River and Big Scrub Flora Reserve along Rocky Creek. The *Castanospermum-Grevillea robusta* alliance occurs along river systems in northeastern New South Wales, including the Richmond and Clarence Rivers, but is not present in the Big Scrub region, where this study was conducted.

Flowering occurs October-November. Fruits are approximately 2 cm by early December, and ripe fruit falls between March and September of the following year. The pod is about 10-25cm long and 4-5cm broad (Boland *et al.* 1984), and has a hard brown woody exocarp. Inside this is a spongy white mesocarp and a thin papery endocarp, within which rest the 3-5 cm diameter seeds. The seeds are large, and round or compressed, each with a shiny thin brown testa. The large woody pods are resistant to decay and when fresh, show a clear cavity where each seed has been produced.

4.3 METHODS

4.3.1 Timing of seed fall

In 1989, three trees were selected at each site to span a range of apparent crop sizes, based on a binocular search of the number of pods in the crown of each tree. To avoid null data for this study, and for a subsequent study of seed predation (Chapter 6), trees which had no seed crop were rejected. For each tree, seedfall was determined at roughly 3-4 week intervals between May-October 1989, based on a count of the number of seed cavities in each pod. Only those pods which lay within the area of the parent crown were recorded. At each visit, the newly fallen ('fresh') pods were marked with paint, using a different colour to identify each sampling interval. To avoid confusion, freshly fallen empty pods were paint-marked in a different manner to undehisced pods. Seed content of fresh undehisced pods (including partly-dehisced pods) was estimated from the undulations on the pod exterior, and corrected at a later sampling date when the pod dehisced. A small, numbered metal tag was pegged in the ground adjacent to each undehisced pod, to allow determination of seed content on subsequent visits (Chapter 6). Few pods disappeared from the site during the year and no additional unmarked pods were detected in later visits to the sites (December 1989/January 1990).

4.3.2 Pod size, and variation in seed crop size

Seed crop size and pod size were determined for the same three trees in each of the five sites in 1989, 1990 and 1991, but additional trees were included in the samples at Big Scrub and Davis Scrub in 1990 and 1991. The additional trees were separated by at least 25 m and were selected to sample a wider area of the forest at each site. In 1989, seed production over time, as sampled above, was summed to give total seed crop size per tree. In 1990 and 1991, pods were collected from beneath each of the trees at the end of the fruiting season (September). Pods were counted, and their seed content was recorded. In general, data on seed crop size and pod size are based on the entire crop for each of the study trees, but a few are estimates based on sampling half or a quarter of the crown's area.

4.3.3 Proportion of population in fruit

Neighbouring conspecific trees >30 cm diameter (dbh) within 20m of the study trees were assessed for presence or absence of a fruiting crop in 1990 and 1991. These data allowed a comparison of the proportion of the population in fruit at the five sites.

4.3.4 Seed weight

Data on seed weight per tree was based on a systematic collection of freshly fallen seeds and pods beneath seventeen trees at Big Scrub and Davis Scrub in September 1991. Damp and damaged seeds which had fallen earlier in the season were excluded. Data on seed weight relative to pod size and seed position in the pod is based on undehisced pods collected from five trees at Wollongbar in 1990, and additional 6-seeded and 7-seeded pods collected opportunistically from Big Scrub and Davis Scrub in subsequent years. The effect of pod size (number of seeds contained in pod) was analysed using one-way analysis of variance, with seed weights pooled within each pod size. (Multiple-factor analysis of variance was not possible due to the differing numbers of seeds per pod.) The effect of individual pod and seed position within the pod, was analysed using two-factor analysis of variance without replication (as each pod is different), for each of pod sizes 2 to 6.

4.4 RESULTS

4.4.1 Timing of seed fall

In 1989, ripe fruit fell between April and September, with an overall peak in May-June (21-74 days after estimated commencement of seedfall, Figure 4.1). There was no clear

difference between sites in timing or pattern of seedfall. Rather, individual trees varied in the distribution of seedfall (Figure 4.2). For trees with a small seed crop, seedfall occurred in a leptokurtic distribution with a peak before mid June (~ 57 days). For trees with a medium to large seed crop, peak seedfall ranged between early June (~ 42 days) and late July (~ 100 days), generally with a marked peak during one sampling interval. Seedfall at Davis tree 3 probably commenced earlier than the other sites, resulting in a large cumulative fruitfall at the first sampling interval (10 May).

4.4.2 Seed crop size

Variation between individual trees, sites and years

Individual trees produced between zero and in excess of 1404 seeds per year (\bar{x} =208 seeds/tree/year), representing 0-456 pods (\bar{x} =82 pods/tree/year). Seed crop size varied between trees and years (Table 4.1). Across all sites, there was no relationship between adult tree size (dbh) and seed crop size for any of the years 1989-1991. Overall, there was a general decline in fruit production between 1989 and 1991, but a few trees maintained or increased their seed crop size over the three years. Total seed production per site from the three trees over the three years, ranged from 2130-3295 seeds and was highest at Johnston's Scrub and Davis Scrub.

Proportion of population in fruit (Fruiting status of nearest neighbours)

At each site, between 48 and 85 % of sampled trees bore at least a small seed crop in 1990 and 1991. Overall fruit production was lower in 1991, and this was evident as a lower frequency of trees with large crops and an increase in trees with no, or small fruit crops (Table 4.2). In 1990, the overall proportion of trees with fruit did not differ significantly between sites ($X^2= 1.7$, $df=4$, ns). However, Wollongbar had a higher proportion of trees with large crops. The overall proportion of trees with fruit was highest at Wollongbar in 1991, compared with individual sites ($X^2> 4.7$, $df=2$, $p<0.1$).

Figure 4.1 Timing of *Castanospermum australe* seedfall during 1989.

(Data pooled for 15 trees across five sites. x axis: Days since seedfall commenced, calculated from 20 April; y axis: Number of seeds.)

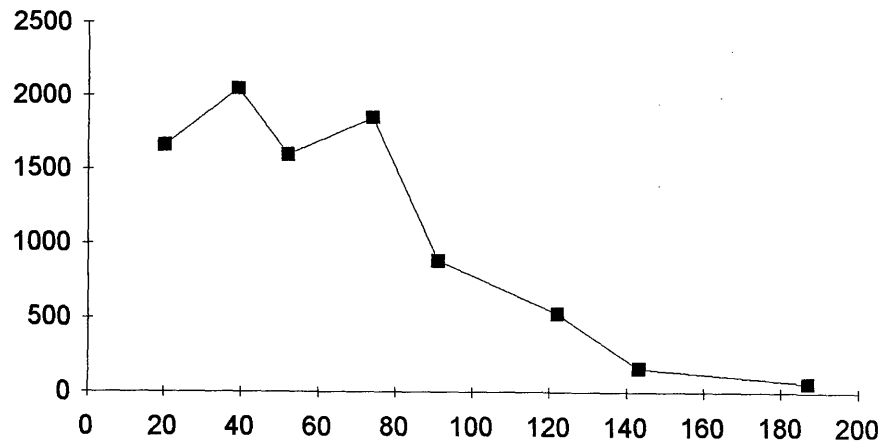
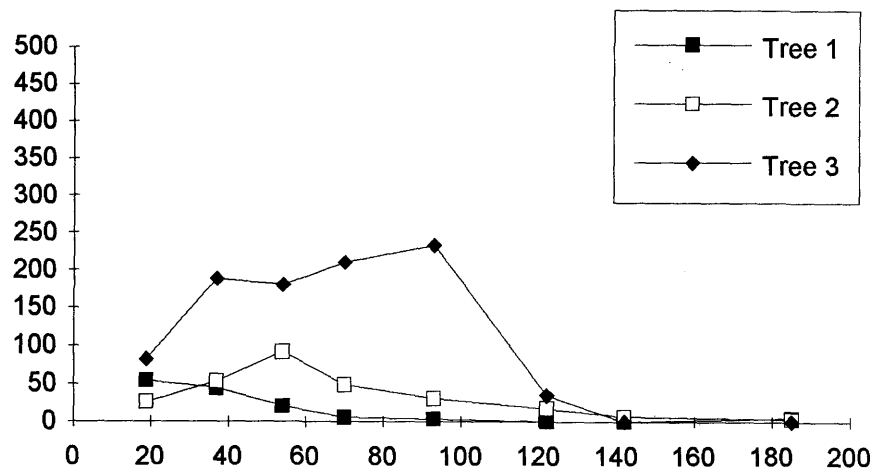
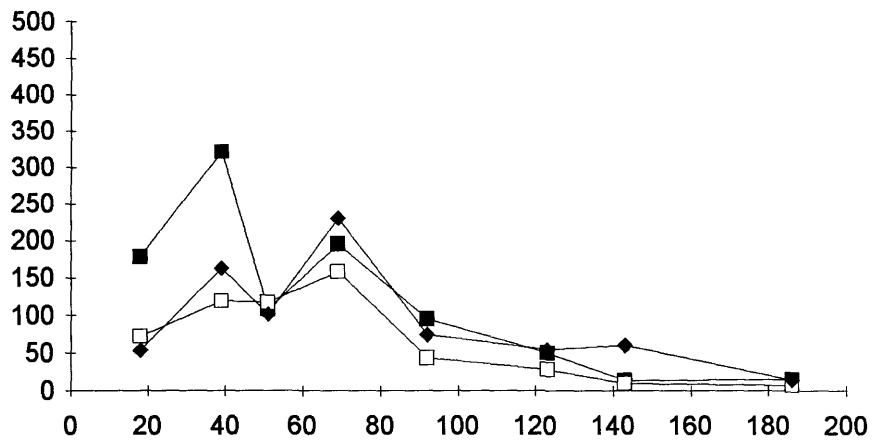


Figure 4.2 Timing of seedfall by individual *C. australe* trees in 1989.

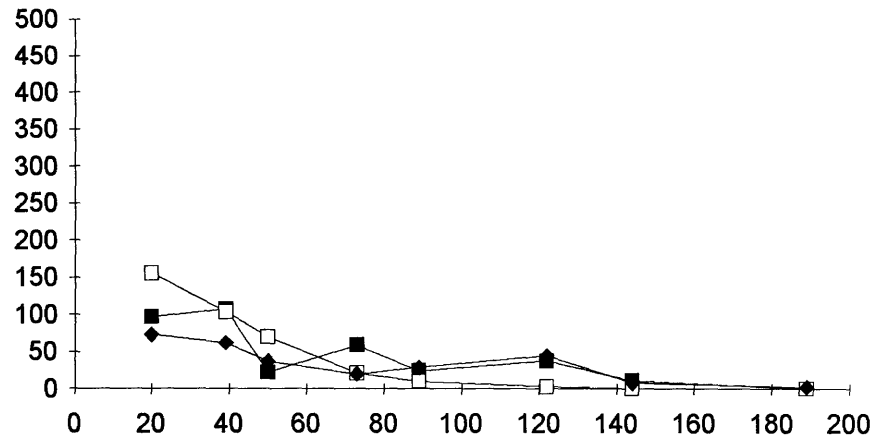
a) Big Scrub



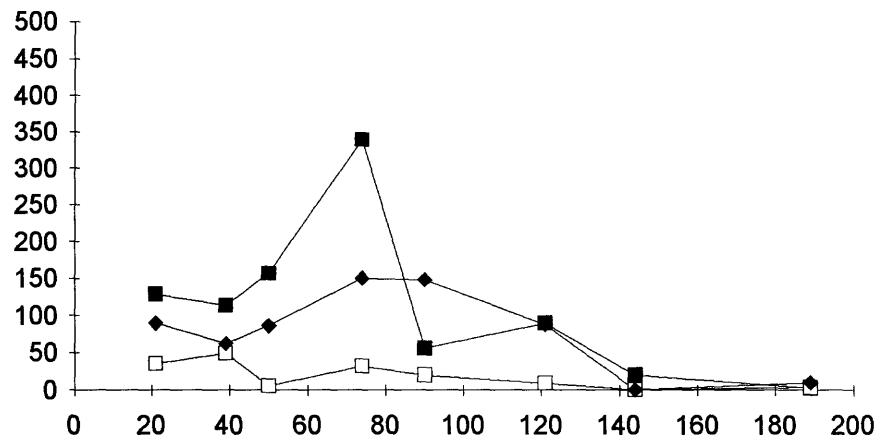
b) Boomerang Falls



c) Johnston's Scrub



d) Wollongbar



e) Davis Scrub

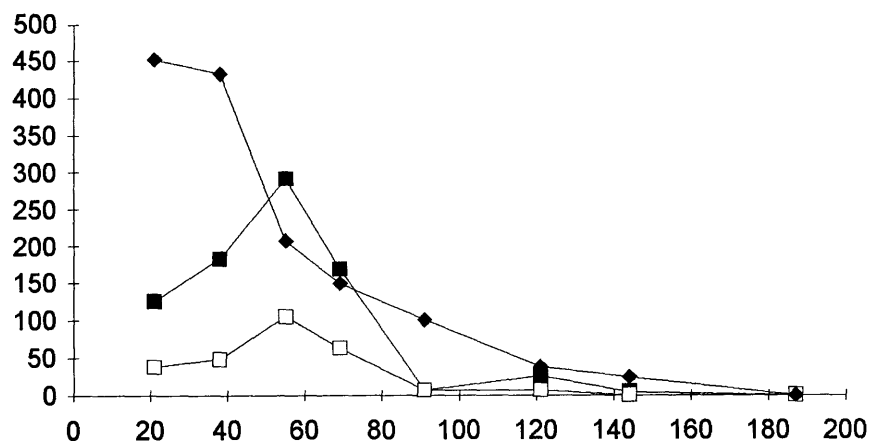


Table 4.1 Annual variation in mean number of seeds produced by three trees per site, 1989- 1991.

(Figures in brackets represent standard deviation. At all sites, the same three trees were sampled each year.)

Site	1989		1990		1991	
BIG SCRUB	447.0	(424.5)	123.3*	(85.6)	139.7*	(132.0)
BOOMERANG	764.0	(211.6)	312.0	(139.5)	22.3	(6.8)
JOHNSTON'S	332.7	(49.2)	588.0	(490.8)	59.0	(71.0)
WOLLONGBAR	564.3	(379.7)	127.7	(6.0)	98.0	(138.1)
DAVIS	826.0	(568.3)	186.0*	(151.9)	2.7*	(3.1)

* At Big Scrub and Davis Scrub, additional trees were sampled after 1989. Mean seedcrop size (and std. dev., number of trees) including the additional trees was: Big Scrub in 1990=211.4 (216.5, 10) and in 1991=127.0 (244, 21); Davis Scrub in 1990=139.4 (161.9, 7) and in 1991=18.3 (32.8, 18). Mean seedcrop size for the three study trees did not differ from the larger sample size, except for Davis Scrub in 1991, when crop size for the three trees was significantly lower (students t-test with unequal variance, $T=1.99$, $df=18.4$, $p<0.05$).

Table 4.2 Percentage of neighbouring conspecific trees with fruit, and crop size

	Big Scrub	Boom	Johnst	Woll	Davis
<u>1990</u>					
Nil crop	25.0	14.8	17.1	23.5	17.9
≤10 pods	38.5	37.0	54.3	5.9	44.6
>10 pods	36.5	48.1	28.6	70.6	37.5
Mean % fruiting	75.0	85.2	82.9	76.5	82.1
<i>n</i>	52	27	35	17	56
<u>1991</u>					
Nil crop	36.4	48.0	47.5	20.0	48.4
≤10 pods	33.3	36.0	45.0	50.0	43.7
>10 pods	30.3	12.0	7.5	30.0	7.8
Mean % fruiting	63.6	48.0	52.5	80.0	51.6
<i>n</i>	66	25	40	20	64

Few trees had crops greater than 100 pods in 1990 or 1991. Data do not include study trees.

4.4.3 Pod size

Individual pods weighed from 54 - 519 g, with a mean of 172.3g ($s=74.36$, $n=137$). Total pod weight was correlated with number of seeds produced (Figure 4.3). Pods contained between 1 and 7 seeds, with an overall mode of two seeds per pod (Figure 4.4). However, the distribution of pod sizes differed between trees, years and sites. In the majority of cases at Big Scrub, Boomerang Falls and Johnston's Scrub, more 2-seeded pods were produced by each tree in each year. For the two large forest sites, there was a strong linear relationship between the number of pods in an individual tree's crop, and the number of seeds produced (Figure 4.5). However, at Wollongbar and Davis Scrub, 50% of the seed crops over the three years showed a higher production of three- or four- seeded pods. This resulted in a marked separation between the sites in the distribution of pod sizes (Figure 4.6). There was no relationship between seed crop size and average pod size per tree (Figure 4.7), nor between tree dbh and mean pod size.

4.4.4 Seed weight

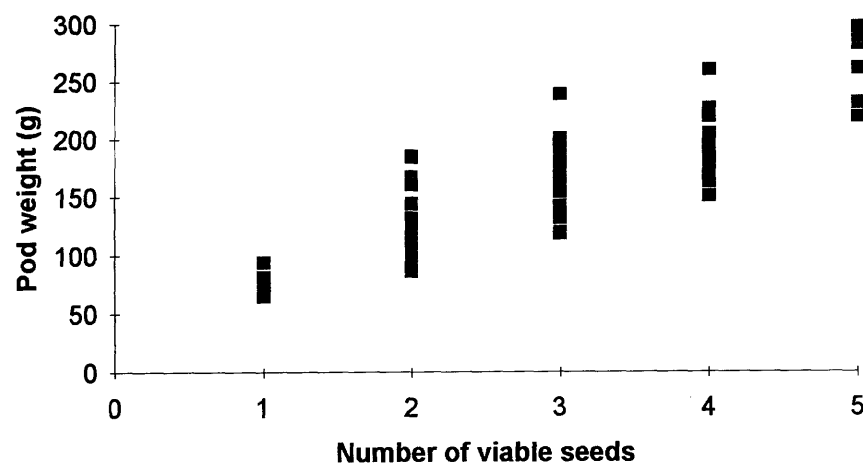
Individual seed weights ranged between 17-93g ($\bar{x}=44.0g \pm 0.4$, $n=993$; Figure 4.8, 4.9). A nested analysis of variance which compared seeds weights collected from 12 trees at Big Scrub and Davis Scrub in 1991, showed a significant effect due to site and tree ($F=14.1$, $df=10$, $p<0.001$; Table 4.3). At least part of this variation may be explained by tree size: Among the trees sampled, smaller trees (dbh) tended to produce smaller seeds on average (Figure 4.10). However there was no relationship between mean seed weight and mean pod size per tree, nor between mean seed weight and seed crop size, for the 17 trees analysed.

Within each pod, seed size is influenced by how many seeds are held in the pod and the seed's position within the pod (Table 4.4). One way analysis of variance showed a significant effect of pod size (number of seeds) on seed weight ($F=4.15$, $df=6$, $p<0.001$). This was due to the tendency for single-seeded pods to produce larger seeds, and 6- and 7-seeded pods to produce slightly smaller seeds on average. Comparison of seed weights between 2-, 3-, 4- and 5- seeded pods did not show an effect of pod size (one-way ANOVA, $F=1.58$, $df=3$, $p=0.19$). Within pods of the same size, there was a significant effect of individual pod on seed weight, for all pod sizes tested (two-factor ANOVA without replication, $p<0.001$, pod sizes 2-6 seeds), that is, differences between individual pods explained more of the variation than differences in seed weight within pods. For 3- and 6-seeded pods only, there was a significant effect of seed position on seed weight (two-factor ANOVA without replication, $p<0.05$, $df=2$; $F=3.14$ and $F=2.58$ respectively). In 3-seeded pods, the seed nearest the stalk showed less variation in weight, and was most often

larger (21 out of 48 pods). In 6-seeded pods, the seed nearest the stalk showed less variation, and was often the lightest. Other positions in the pod were more variable in weight.

Although seeds held in small pods tended to be larger, some individual seeds held within many-seeded pods (e.g. 5 or 6-seeded) were equally as large as those in smaller pods. In multiple seeded pods, the distribution of seed weights was variable. For example, although the mean weight of seeds in position one and two in two-seeded pods did not differ, within individual pods, the seeds were rarely of equal weight. Pods were fairly evenly divided between those where the terminal seed was larger (n=16) and those where the seed nearest the stalk was larger (21). Within 3-seeder pods, the average weight of the seeds also did not differ significantly with pod position (one-way ANOVA, $F=0.67$, $df=2$, $p=0.5$). In only one third of individual 3-seeder pods was the middle seed larger, despite the higher average. Rather, the slightly higher mean weight of the middle seed was an artifact of a greater variability in weight of the terminal seed. Within individual 4-, 5- and 6-seeded pods, the middle seeds were variable in weight, but at least one of them was markedly heavier than both of the end seeds: in only four out of 36 pods were one of the end seeds larger than those in the middle.

Figure 4.3 The relationship between total pod weight and seed content (number of viable seeds held within pod).
(data are from pods collected at Wollongbar in 1990)



Regression $y = 42.07x + 35.735$, $p < 0.001$, $R^2 = 0.70$.

Note: Some larger pods were found at Big Scrub and Davis in subsequent years, and indicate that the slope of the regression may change between years or sites.

Figure 4.4 Distribution of pod sizes, pooled for five sites over 3 years. (3-11 trees per site sampled each year 1989-1991)

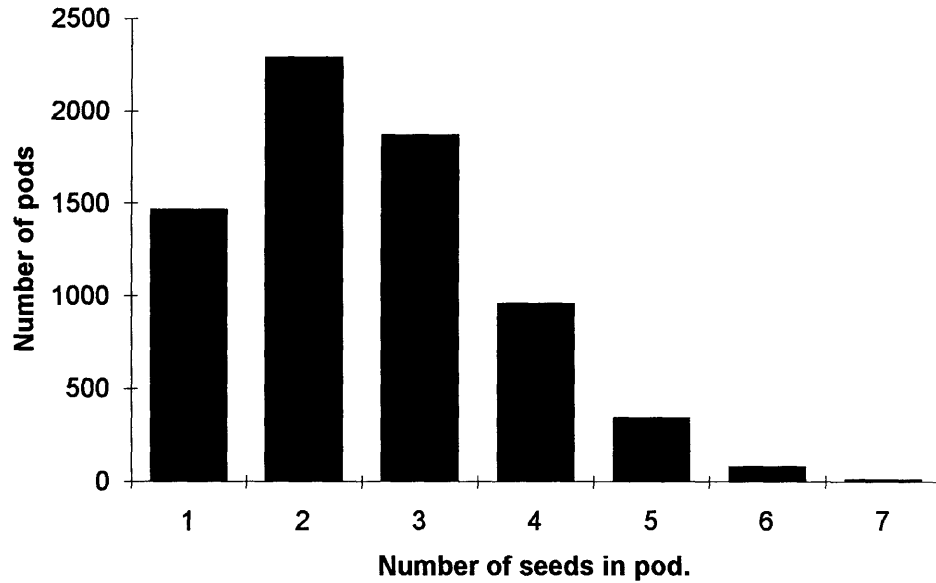
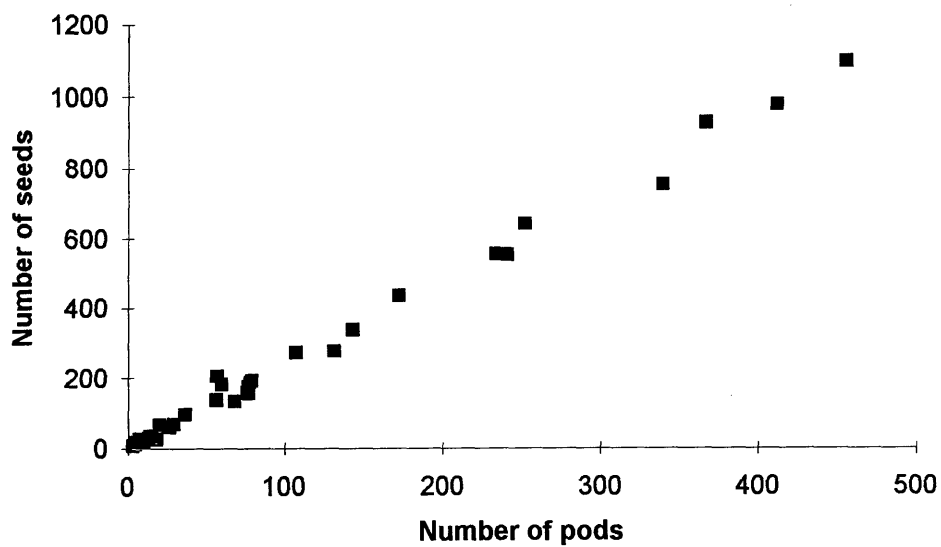


Figure 4.5 Relationship between number of pods and seeds produced per tree for a sample of trees at Big Scrub and Boomerang Falls (1989-1991).



$$(y=1.98+2.37x, r^2=0.99)$$

Figure 4.6 Percentage of pods of each size at five different sites (1989-1991).
(data pooled for three trees at each site)

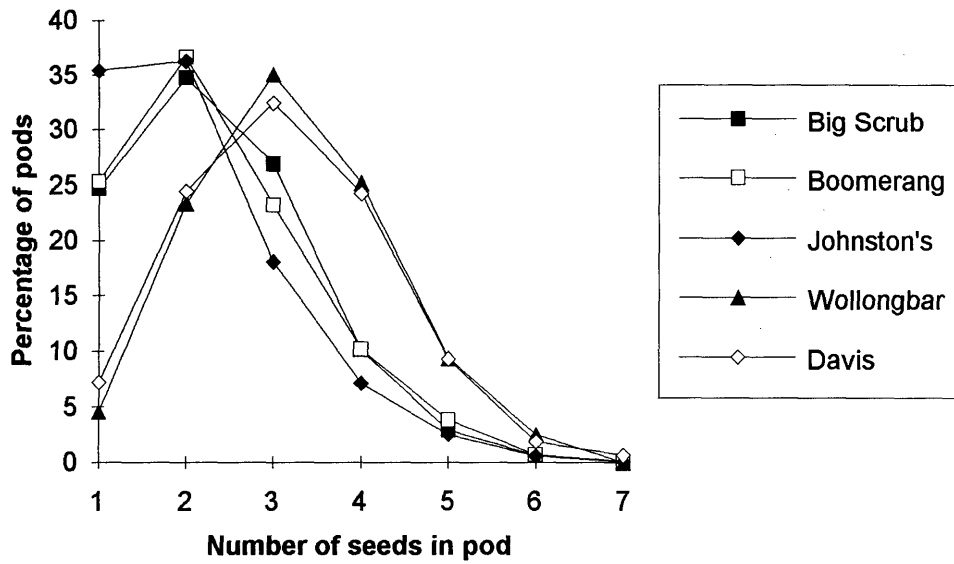


Figure 4.7 Relationship between seed crop size and average pod size per tree.
(data from trees at five sites 1989-1991)

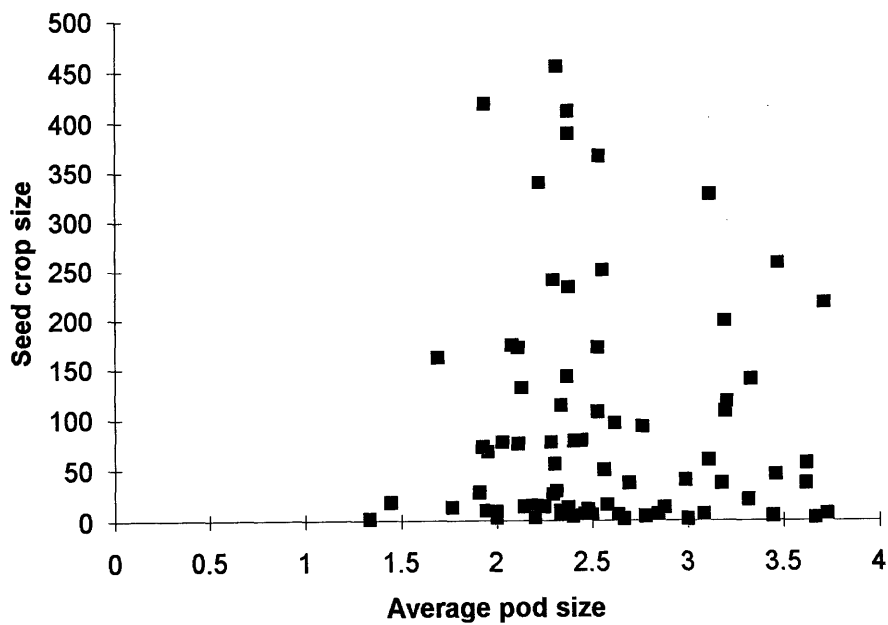


Figure 4.8 Range of seed sizes of *Castanospermum australe*.
(scale = 1 cm)



Photography: Media Resources Unit, University of New England

Figure 4.9 Distribution of seed weights (pooled samples from Big Scrub, Davis Scrub and Wollongbar; n=993 seeds)

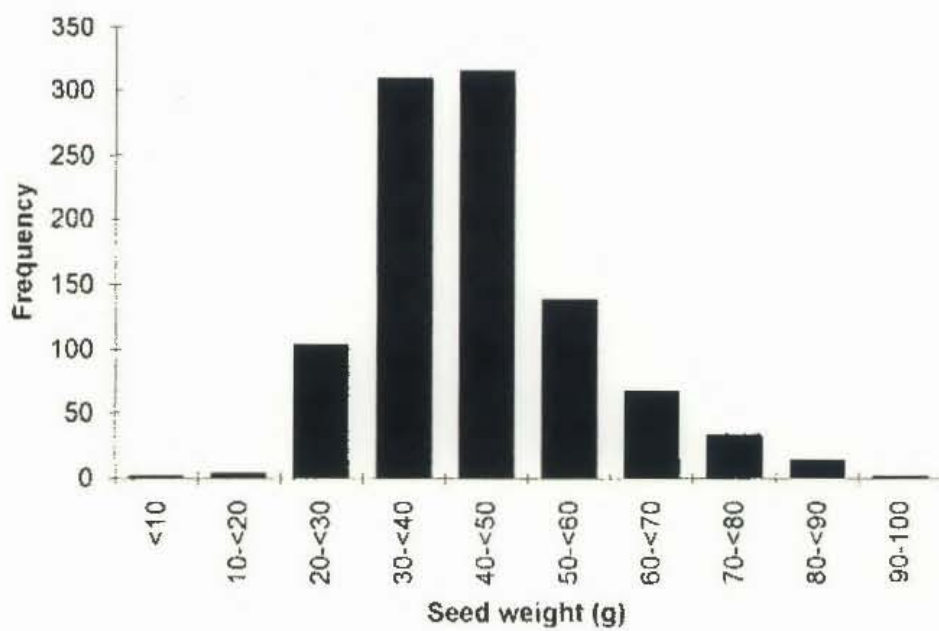


Table 4.3 Average seed weight per tree for a sample of trees from Davis Scrub and Big Scrub F.R. (1991).

Site	Tree No.	Mean seed weight	No. seeds	Std. dev.
Big Scrub	2*	44.3	48	8.8
	5*	58.2	15	12.2
	10*	38.9	175	8.1
	10A	52.8	15	8.6
	15*	49.3	40	10.2
	17*	68.4	36	14.0
	18*	58.3	34	15.8

No. sampled, mean seed wt.	7	46.9	363	14.1

Davis	1	64.1	6	12.8
	3	43.4	2	6.4
	6*	49.6	53	8.5
	7	43.3	3	10.0
	8&9	41.8	9	9.4
	10*	40.9	16	8.5
	12*	43.1	25	7.7
	13*	38.0	26	6.7
	17*	52.1	39	11.5
	18*	45.5	25	9.1

No. sampled, mean seed wt.	10	46.5	204	10.6

* Nested ANOVA based on 15 seeds from each of 6 trees per site showed a significant effect on seed weight due to site ($F=38.9$, $df=1$, $p<0.001$) and tree ($F=14.1$, $df=10$, $p<0.001$). Mean dbh of trees at Davis less than Big Scrub. See Figure 4.11.

Figure 4.10 Relationship between tree trunk size (dbh) and mean seed weight for 17 trees sampled from Big Scrub and Davis Scrub in 1991.
($y=0.117x + 38.29$; $r^2=0.34$; regression $F=7.69$, $df=1,15$, $p=0.014$)

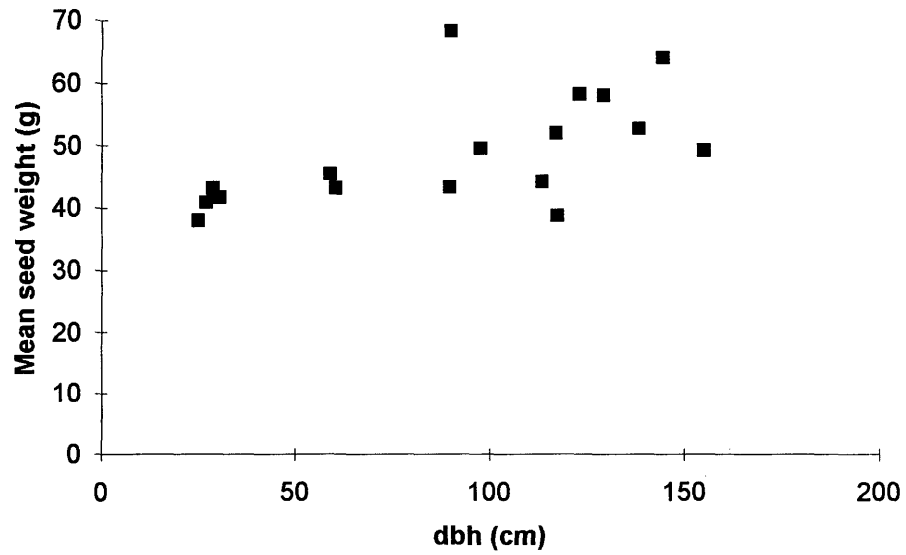


Table 4.4 Average weight of seeds within pods of different sizes (most pods collected from Wollongbar 1990, Big Scrub 1991).
(Mean weight (g) \pm SE. Seeds numbered from terminal tip of pod towards stem.)

Pod (empty)	SEED POSITION							n (pods)	
	Seed 1	Seed 2	Seed 3	Seed 4	Seed 5	Seed 6	Seed 7		
POD SIZE									
1-seed pod	29.4 \pm 1.8	52.2 \pm 5.6						8	
2-seed pod	38.3 \pm 2.2	42.4 \pm 1.9	*42.3 \pm 1.5					38	
3-seed pod	45.2 \pm 0.9	39.6 \pm 1.5	42.0 \pm 1.4	*40.6 \pm 1.4				51	
4-seed pod	51.7 \pm 2.8	37.2 \pm 3.1	*42.5 \pm 3.5	39.8 \pm 3.1	36.8 \pm 3.0			19	
5-seed pod	75.1 \pm 14.1	37.7 \pm 2.5	43.4 \pm 2.2	*46.7 \pm 4.2	46.2 \pm 5.7	41.0 \pm 5.6		8	
6-seed pod	72.4 \pm 5.3	33.7 \pm 4.7	35.6 \pm 4.5	*37.1 \pm 4.0	*39.1 \pm 4.9	37.6 \pm 4.2	31.4 \pm 2.8	11	
7-seed pod	75.2	31.4	33.8	30.8	*36.6	35.6	41.0	38.3	1

* seed position most often heaviest in pod.

Overall mean weight for seeds from pods of different sizes : 1-seeded pod 52.2g \pm 5.6 (s.e), 2-seeded 42.4g \pm 1.2, 3-seeded 40.7g \pm 0.8, 4-seeded 39.1g \pm 1.6, 5-seeded 43.0g \pm 1.9, 6-seeded 35.7g \pm 1.7, 7-seeded 35.4g \pm 1.4.

4.5 DISCUSSION

4.5.1 Timing of seed fall

In *C. australe*, seeds are released from the tree over a 6-7 month period of the year (March-September) and germinate during the rainy season (December-April) that follows seed fall (Chapter 8). Such a pattern appears common in rainforest, where fruit fall tends to peak just prior to the rainy season, apparently to allow optimum conditions for germination (Garwood 1982, Foster 1982). Although *C. australe* seed fall occurs during the dry season, the large seed size apparently gives it the reserves to last until the rains commence, thus maximising the moisture conditions for seed germination and seedling establishment. Foster (1982) suggested that heavier seeds may fall more often in the late rainy season, rather than in the early rainy season, because larger seeds or seedlings can cope better with drought. (However, this may only be true amongst moist-seeded species which land in shaded conditions within tropical forests. Those heavy seeds which fall in drier forest types, or within a gap in moist forest may be prone to desiccation during the dry season.)

C. australe may also be optimising its chances of pollination, by flowering in the early rainy season when birds and bats may be more abundant in the region. If this were the case, then time until seed maturation may have been a less important selective force than pollination.

Peak seed fall precedes the coldest months (June-August). There tend to be fewer species in fruit in subtropical rainforest in winter-spring than in summer-autumn (Holmes 1987, Innes 1989, Stewart 1995), and the large seeds are potentially an important food source, at least in most years, to fauna able to detoxify the alkaloid within the seed. It is plausible that winter seedfall increases the opportunity for seed dispersal, by ensuring that seeds are available for removal by mammalian vectors (Chapter 7), or streams swollen with subsequent heavy rain events.

4.5.2 Seed crop size

Annual and individual variation in seed crop size

In *C. australe*, seed production showed up to a nine fold difference between 1989 and 1991. This marked annual variation in seed production seems typical of tropical shade-tolerant tree species (Schupp 1990 and references within, Wheelwright 1986; see Table 4.5). Differences between years are often two to five-fold, but may reach up to 400-fold in mast fruiting species such as *Faramea occidentalis* (Schupp 1990). This may be a response to climatic factors (Rathcke & Lacey 1985, Schupp 1990) and/or to trade-offs in resource allocation between fruiting seasons (see Ashman 1992). Fruit production in *C. australe* also varied between and within individuals, suggesting that individual trees may produce large crops every few years, as has been noted for other tropical tree species (e.g. Becker & Wong 1985, Wheelwright 1986). Due to the non-random selection of trees with moderate-to-large crops in 1989, there is insufficient data in this study to identify whether some trees are generally more fecund, or whether individual trees vary in which year they produce a large crop.

Fruiting synchrony

In *C. australe*, nearest neighbour data indicated that 48-85% of trees produce at least some fruits each year. The lower average fruit production in 1991 corresponded with a decline in fruit production for most trees, and an increase in the proportion of trees with no fruit. This is consistent with observations of other tropical tree species. In a seven-year study of fruiting in Lauraceae, Wheelwright (1986) found that typically, 40-80% of the population of each species produce fruit in a given year. Although there was synchrony within species in

the timing (season) of fruitfall, there was between-year asynchrony in fruit production. Different trees reproduced in different years. Individual trees also differed in fecundity and the regularity of their reproductive cycle. Similarly, Janzen's (1978) observations of fruiting behaviour of *Hymenaea courbaril* (Leguminosae) at several sites in Costa Rica, showed that not all trees produced fruit each year, and that seed crop size varied greatly between years. At all but one site, some trees produced fruit every year. In 'heavy' years, more trees produced fruit and some of these trees produced large crops. In 'poor' years, very few trees produced crops and individual-tree crops were often small. However, trees differed in their reproductive cycle, and those which produced fruits in poor years were generally not those producing large crops at other times. Individual trees had 'lay' years between large crops, during which they were probably regaining resources. Janzen (1978) hypothesized that *H. courbaril* has to store resources for a number of years in order to produce a sufficiently large crop to satiate flower bud and pre-and post-dispersal seed predation, and to allow some seedlings to survive.

C. australe flowers annually, and appears to produce a crop each year (A. Floyd pers comm.). Seed production may sometimes be higher than that recorded during this study, depending in pollination and climatic events. For example, the species is reputed to have fruited heavily in northeastern New South Wales in 1987 (P. Recher pers. comm.). The results of the nearest neighbour and fruit crop size measures indicate that if heavier fruiting does occur, it will represent a higher proportion of the population in fruit, and a larger seed crop per tree. In 1989, the season of fruit fall was synchronous between trees, however individual trees varied in the timing of peak seed release. This resulted in several months in which large numbers of seed were available at each site. The variation between individual trees and between years in fruit crop size is likely to have important implications for predator satiation, level of seed predation, and level of seedling establishment in this species.

Fruit biomass

Based on an average seed weight of 44 g, individual trees produced between 0 and in excess of 61.8 kg of seeds per year. When average pod weight is used (172.3 g), trees produced between 0-78.6 kg of fresh fruit biomass/year. Compared with a range of canopy-dominant temperate tree species (figures obtained from Greene and Johnson 1994, see Table 4.6), average seed production per tree for *C. australe* and other tropical species is high. Seed output by *C. australe* is equivalent to *Virola surinamensis*, a canopy emergent tree of neotropical rain forest. *Virola surinamensis* produces seeds with a fleshy aril, and individual trees produce 1.2-83.2 kg in seed biomass (see Table 4.6). This is based on

3.18g seed fresh weight, excluding the fruit exterior and fleshy 1.59 g aril (Howe & Vande Kerckhove 1981). In comparison, average seed production by *C. australe* is higher than that recorded for *Hymenaea courbaril*, a large-seeded legume tree species of Costa Rican lowland dry forest.

4.5.3 Pod and seed size

In *C. australe*, seed weight varied within and between pods, and between trees. Variation in seed size is probably a result of three main factors: Resource availability, the shape of the pod, and tree size. For larger pods, at least one of the seeds in the middle is largest, the seeds on the end presumably confined by the tapered shape of the pod. This aside, the results indicate that on average, seeds receive sufficient nutrient to form similar-sized seeds across most pod sizes, with the seed nearest the stalk having a slightly higher chance of being larger. There was evidence that smaller adult trees tend to produce smaller seeds, and do not produce large seed crops.

Initially, it was thought that seed size has lower phenotypic and genetic variability in comparison with many other plant characters less closely associated with plant fitness (Harper 1977, Primack & Antonovics 1981). More recent studies, based on individual seed weights rather than mean weight of large numbers of seeds, have shown that there is considerable variation in seed size, including within individual plants (Fenner 1985, Bazzaz & Ackerly 1992). Much of the variation is a result of positional effects during development, such as the sizes of successive seeds in pods of many legumes (Wulff 1986). There may also be substantial capacity for phenotypic plasticity in seed size in response to environmental variation (Winn 1988, Winn & Werner 1987).

Up to 16-fold variation in seed size has been found within a number of tropical trees species (e.g. Howe & Richter 1982; Dirzo and Dominguez 1986). The range of seed weights obtained for *C. australe* is very similar to that obtained for another large-seeded tropical legume *Eperua grandiflora* (Caesalpinaceae) in French Guiana (Forget 1992a). Such a range in seed sizes is likely to have important implications for seed and seedling survival. The maintenance of a range of seed sizes within a species may be an adaptation promoting both seed escape from seed predation (small seeds) and seedling vigour (large seeds) (e.g. Moegenburg 1996). The range of seed sizes within a pod and within an individual tree may help ensure that only some seeds are eaten per pod. Assuming that seeds within a pod are more genetically related than between pods (due to pollen deposition by pollinators), size-dependent seed predation could ensure that single seeds survive from a range of pods and maximise the genetic variability of seeds which escape predation. The range in size of seed

reserves may also promote a range of germination times, therefore bet-hedging for unpredictable early rains in tropical forests with a distinct wet and dry season (see Chapter 8).

In addition to overall seed size, individual trees may alter their resource allocation in terms of number of seeds matured per pod, and crop size. Why the sites differed in average pod size (seed content) is not known. As there is no relationship between dbh and mean pod size per tree, the cause is likely to be resource or pollinator limitation, with the higher seed set per fruit at the small sites reflecting increased exposure near the forest edge. However, whether the trees differed in ovule number per flower, and pollinator visitation must be determined before the implications of differential pod size between sites can be interpreted.

4.5.4 Conclusions

Individual *C. australe* trees vary their investment in seed production from year to year, and overall production per population is higher in some years, probably as a result of differential pollinator abundance and resource availability. However, across the three years and the three trees studied per site, total seed production was similar between sites. Fruit crop size and average biomass of seed production is consistent with other tropical tree species, and represents a large potential food source to predators able to detoxify the seeds, particularly as seeds fall during winter when the availability of other fruit resources is lower. Seed size differs between trees and within and between pods, and this variation has implications for level of predation, and level of seedling establishment.

Table 4.5 Fruit crop size of selected large-fruited tropical species

Species	No. fruits per tree per year	No. trees	Fruit diam. (cm)	No. seeds per fruit	Seed size (cm)	Seed weight (g)	Source
<i>Eperua grandiflora</i> (Caesalpinaceae)	~738 100-1700	1 7	10	1-2	7x6x3	47.6	Forget 1992a Sabatier 1983
<i>Dipteryx panamensis</i> (Leguminosae)	3.3/m ²	19	5	1	4		de Steven & Putz 1984
<i>Hymenaea courbaril</i> (Leguminosae)	0-1000	175	3-10	1-15	1.5x2	2-6	Janzen 1978, Hallwachs 1986
<i>Aglaia</i> sp. (Meliaceae)	50-490	1	6-8	2	4.5x2.7		Becker & Wong 1985
<i>Macoubea guianensis</i> (Apocynaceae)	20-40	4	10	100- 300	0.5		Notman <i>et al.</i> 1996
<i>Pouteria</i> sp. (Sapotaceae)	2000- 3000	4	2x4	1	1x3		Notman <i>et al.</i> 1996
<i>Virola surinamensis</i> (Myristicaceae)	214- 26163	25	~3	1	2x1.5	3.2	Howe & Vande Kerckhove 1981, Howe 1983.
<i>C. australe</i>	0-456	42	4-5	1-7	7x5.5	44.0	this study

Upper size limit is given for fruit diameter and seed size.

Table 4.6 Average annual biomass (weight) of seeds produced per individual tree for a range of temperate and tropical species .

(Seed production averaged over at least 3 years for several trees.)

	No. seeds per year/ individual tree	seed weight (mg)	Mean total seed biomass per year (kg)	Source
<u>Temperate</u>				
<i>Betula papyrifera</i>	27239	0.6	0.016	Bjorkbom 1971
<i>Pinus ponderosa</i>	2667	37.7	0.1	Fowells & Schubert 1956
<i>Quercus prinus</i>	107	4535	4.85	Downs & McQuilkin 1944
<u>Tropical</u>				
<i>Virola surinamensis</i>	214 - 26163	3180	1.22 - 83.2	Howe 1983
mean	4884		15.53	
<i>Hymenaea courbaril</i>	0 - 4500	~4000	0 - 18	Janzen 1978, Hallwachs 1986
mean (Sendero Natural Group)		88.3	0.35	
<i>Castanospermum australe</i>	0-1404	43998	0 - 61.78	this study
mean	208		9.17	

Chapter 5. IDENTIFICATION OF PREDATORS OF *CASTANOSPERMUM AUSTRALE* SEED.

5.1 INTRODUCTION

Studies of the effect of seed predation and dispersal on plant population survival and distribution require that the suite of seed predators and dispersers be identified. Insect predators are generally identified by examining diaspores collected pre- or post-dispersal (e.g. Andersen 1989). Several techniques allow detection of actual seed predation by mammals on rainforest seeds. Here, predation is defined as damage by chewing or feeding, to all or part of a seed's tissue. In the neotropics, field observation of feeding behaviour is the most common technique for study of diet selection and seed dispersal in diurnal arboreal mammals such as monkeys (e.g. Estrada & Coates-Estrada 1986, Galetti & Pedroni 1994). In Australian rainforest, a combination of observation, radio-tracking and placing seed traps under colonies has been used for studies of diet and potential seed dispersal by flying foxes *Pteropus* spp. (McWilliam 1986, Richards 1990, Parry-Jones and Augee 1991a, Eby 1991 a, Eby & Palmer 1991) and the Queensland Tube-nosed Bat *Nyctimene robinsoni* (Spencer & Fleming 1989). These animals are noticeable because of their large, vocal groups at roosting sites during the day. However most Australian rainforest mammals are nocturnal, arboreal or scansorial, and relatively solitary, and are difficult to observe feeding (but see Procter-Gray 1984, Goudberg 1990). Most dietary information has been obtained from stomach or faecal analysis. Observation of feeding behaviour and faecal analysis are time-consuming, and are prohibitive within the scope of a broader study of seed ecology. In addition, fruit and seed tissues, once masticated and digested, are often difficult to identify to species (Pahl 1984, Carron *et al.* 1990), and obtaining stomach contents has sampling and ethical problems associated with killing what may be uncommon animals.

Several alternative techniques test for the potential for seed consumption by animals (although the animals may not actually eat the seed in all situations). Feeding trials identify potential predators by keeping animals in captivity and offering them selected seeds (e.g. Estrada & Coates-Estrada 1986). Field methods include the use of smoke boards or sand plots to identify the feet of animals (Miranda & Dirzo 1991), which have inspected fruit placed in the centre of the plot. Exclosures of differing permeability (access) can be used to compare seed removal rates by different sized fauna (Brown & Davidson 1977, Brown *et al.* 1979, Terborgh *et al.* 1993, Terborgh & Wright 1994). Additionally, some seed predation studies have included a small mammal trapping survey underneath the fruiting trees. Either standard baits are employed, to verify the relative abundance of small

mammals in the forest (Janzen 1986, Gonzalez-Espinosa & Quintana-Ascencio 1986, Telleria *et al.* 1991), or the target fruit is put in traps, to test which animals will investigate seeds (Janzen 1986, Estrada & Coates-Estrada 1986, Coates-Estrada & Estrada 1988, Lott & McIntyre 1991). Interpretation of an animal's response to fruit placed in traps is complicated by three factors: 1) animals differ in relative trappability and curiosity, 2) seed damaged in frustration whilst inside the trap may be indistinguishable from seed eaten by choice, and 3) if seed is abundant outside the trap, predators may not enter the trap to get one or a few seeds. In contrast, laboratory trials allow comparison among mammal species and individual animals in their response to fruit species.

Information can also be gained from careful observation of seeds and fruits on the forest floor. Hard seeds (e.g. legumes), nuts, and drupes and berries with a firm skin, rind, or seed are likely to be marked by teeth and claws (e.g. see Burbidge & Whelan 1982). Such seeds chewed by mammals can often be distinguished from those damaged by insects or birds (e.g. Nilsson & Wastljung 1987, Santos & Telleria 1994). Further, if incisor and claw marks are distinguishable between vertebrate species, these marks are suitable for identification of the specific (actual or potential) seed predators and dispersers.

This study used a combination of literature review, inspection of field-collected seeds and a small mammal feeding trial to identify potential and actual predators of *Castanospermum australe* seed (Black Bean). *C. australe* seeds contain 0.3% castanospermine and are generally toxic to eutherian mammals (Elbein & Molyneux 1987). However, field observations indicated that insects and at least two mammal species eat the seeds in subtropical rainforest of the Border Ranges and Big Scrub (Floyd 1990a, E. Date pers. comm., R. Lott pers. obs). Prior to this study, the predators had not been identified. The above techniques were chosen because the seeds of *C. australe* are large and readily observed, and the cotyledons are sufficiently hard to retain teeth marks.

5.2 CASTANOSPERMUM AUSTRALE SEED CHARACTERISTICS AND POTENTIAL SEED PREDATORS

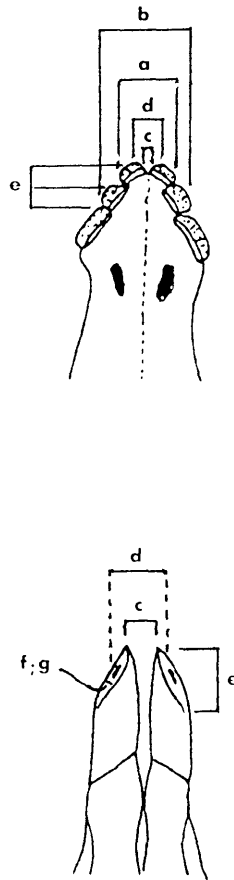
Castanospermum australe produces hard, green-brown, dehiscent, woody pods, each containing one to several large brown seeds (mean seed weight $44.0\text{g} \pm 0.4$, $n=993$). The fruit and seeds exceed the size, and lack the fleshy layer or appendage, which are usually the attractions to birds (van der Pijl 1972, Howe 1986, Clifford & Drake 1981, Forde 1986) and reptiles (Satrawaha & Bull 1981, Dubas & Bull 1991, Cogger 1992), and the cotyledons are too hard for consumption by any means other than gnawing. The seed's hardness requires an animal with a dentition capable of gnawing. Amongst the mammals,

this would require an animal of sufficient size to be able to manipulate the seed. A review of natural history texts and dietary studies (e.g. Harrison 1962, Redenbach 1982, Watts & Aslin 1981, Strahan 1983, Walton & Richardson 1989) showed that a range of Australian rainforest mammals are at least occasional seed predators and dispersers, but for most mammals, the information on actual diet and quantity of seeds and fruits eaten is scant. These data were only sufficient to identify several potential predators of *C. australe* seed, and it was necessary to investigate further which mammals actually eat the seeds. Based on habitat choices, broad diet, tooth structure and size, the most likely predators of *C. australe* seed in northeastern NSW are: the Mountain Brushtail Possum or Bobuck *Trichosurus caninus*, Red-legged pademelon *Thylogale stigmatica*, Red-necked pademelon *T. thetis*, Fawn-footed Melomys *Melomys cervinipes*, Bush Rat *Rattus fuscipes*, and Black Rat *R. rattus* (Chapter 3). Whether these species actually eat *C. australe* seeds is tested in this chapter.

5.3 METHODS

5.3.1 Patterns of damage by insects

Types of seed damage by insects were described from seeds collected from the forest floor. In July 1990, a sample of fresh undehisced pods was collected from four remnants of subtropical rainforest near Lismore, northeastern New South Wales (Big Scrub F.R., Boomerang Falls F.R., Davis Scrub, Wollongbar). These were opened and the seeds inspected for insect damage and decay. Insects found in the seeds and pods were collected and preserved. At the same time, a separate sample of seeds lying on the forest floor and damaged by insects was preserved in 70% alcohol. Insects which emerged into the collecting jar or were dissected from the seeds were sorted for identification. Insects found eating fresh firm seeds were identified. Otherwise, no attempt was made to determine which insects were responsible for the different kinds of damage, although some qualitative observations were made. No attempt was made to investigate effects of season on insect seed predation. Coleoptera specimens are lodged with CSIRO Division of Entomology, Canberra, and all others with the Division of Entomology, Department of Primary Industries, Indooroopilly. Specimen reference numbers (R. Lott) are indicated in parenthesis below, and a full list of references numbers and identification details to date are shown in Appendix 1.

Figure 5.1 Diagram of measurements made on skulls

Measurements: a) Width of first 2 incisors (front teeth), b) total width 4 teeth, c) distance between incisors, d) distance between 'peaks', e) cutting arc of front incisors, f) cutting depth of front incisors, g) tooth thickness.

5.3.2 Patterns of damage by mammals : Observations of eaten seeds

Seeds that had naturally fallen to the forest floor were examined at five sites: Big Scrub F.R., Boomerang Falls F.R., Johnston's Scrub, Davis Scrub, Wollongbar. At three to four week intervals between May and October 1989, all seeds under three *C. australe* trees at each of the five sites (n=8441 seeds) were examined as part of a study on seed survival (Chapter 6). During field work, freshly-eaten seeds were inspected opportunistically for tooth marks and patterns of seed predation. Representative seeds with the clearest tooth marks were collected and matched with skull specimens of *T. caninus*, *T. stigmatica*, *T.*

thetis, *R. fuscipes* and *M. cervinipes* held at the Department of Ecosystem Management, University of New England. Skulls were matched with teeth marks in seeds by three means: Firstly, upper and lower jaws were inserted into teeth marks in seeds. Secondly, the upper and lower jaws of the diprotodont species were firmly placed against a ball of plasticine, to give the impression of each set of teeth. The resulting patterns were compared with those on seeds. Thirdly, measurements made of teeth marks in seeds were compared with measurements of upper and lower incisors on skulls (Figure 5.1). Teeth were measured at the angle at which they were expected to contact the seed.

5.3.3 Feeding trials

In July 1990, a feeding trial was conducted to determine which captive mammal species would eat *C. australe* seed, when provided with a choice of fruits and seeds present in their natural environment. Animals were obtained from a small mammal live-trapping survey (section 5.3.4) conducted in the five remnants. All sites were of the *Castanospermum-Dysoxylum muelleri* vegetation suballiance (Floyd 1990b), and animals captured should have been familiar with *C. australe* seed as a potential food source. Two *T. caninus*, two *R. rattus*, five *R. fuscipes* and five *M. cervinipes* were retained from this survey and held in cages for 2-4 days. No *Thylogale* spp. were captured. Animals were housed in separate cages in an enclosed room with a cement floor. Newspaper was placed beneath cages, and in addition, *T. caninus* cages were placed over a fine mesh and tray. This arrangement insulated the floor, prevented loss of food, but drained excrement. Newspaper was provided within cages for nesting material, each cage was insulated with newspaper and hessian, and the room was heated during the night (17°C day, 14°C night). Animals were fed daily with commercial rat pellets (rodents 9-11g, *T. caninus* 66-100 g; Appendix 4), a portion of apple, and water was provided *ad libitum*. In addition, *T. caninus* were offered kiwi fruit, banana, bread, nuts and cauliflower leaves (some of these items are eaten by them in southeastern Queensland (van Dyck 1979)). On the final day, cages were cleaned and food pellets removed, and animals were given a cafeteria of rainforest fruits collected from the field sites at the time of animal capture. The number and weight of fruits was determined prior to introduction into the cage. The cafeteria was available to each animal for approximately 24 hours. At the end of the trial, animals were released at night at the point of capture.

In an attempt to ensure that animals had sufficient palatable food as an alternative to *C. australe* seed, non-toxic species thought to be palatable to most mammals were included in the feeding trial. These were ripe fruits of *Ficus watkinsiana*, *Acmena brachyandra* and water vine *Cissus* sp, and cracked and uncracked *Macadamia* seeds. It was assumed that

all animals would consume a portion of these palatable fruits and seeds, and this would meet their daily food-weight requirements (e.g. 15g/rat for 203-482g rats, National Research Council 1978), based on each animal's body weight. The full list of species of fruit and seed provided is shown in Table 5.1. Included in the cafeteria were three *C. australe* seeds per rodent, and six per *T. caninus*. Both freshly fallen and early-season ('old') *C. australe* seeds were included.

Table 5.1 Fruit species and weights offered to captive wild animals in feeding trial.

Species	Ave wt. given rats (g)	Number of fruits	Ave wt. given <i>T. caninus</i> (g)	Number of fruits
<i>Ficus watkinsiana</i> (ripe)	22.8	1	298.0	14.5
<i>F. watkinsiana</i> (green)	15.0	1	52.4	4
<i>Ficus superba</i> (green)	9.4	2	10.8	2
<i>Acmena brachiandra</i>	36.9	2	196.6	11
* <i>Macadamia</i> (uncracked)	6.7	1	7.4	1
* <i>Macadamia</i> (cracked)	6.4	1	12.2	2
<i>Cissus</i> sp.	9.6	9	10.8	10
<i>Solanum mauritianum</i> (ripe)	0.8	1	1.1	2
<i>S. mauritianum</i> (green)	1.6	2	3.2	4
<i>S. pseudocapsicoides</i>	1	1	0.8	1
<i>Citriobatus pauciflorus</i>	0.6	1	0.5	1
* <i>Millettia australis</i>	6.7	2	8.2	3
<i>Cordyline rubra</i>	2.2	5.1	4.9	10
<i>Pittosporum undulatum</i>	3.4	2	12.6	8
<i>Cinnamomum camphora</i>	6.0	10	11.7	20
<i>C. australe</i> pod (<i>T. caninus</i> only)	-		235.5	1
* <i>C. australe</i> (fresh, Johnstons)	46.2	1	109.9	2
* <i>C. australe</i> (fresh, Davis)	52.2	1	110.2	2
* <i>C. australe</i> (old, Davis)	49.5	1	100.9	2
Average total weight	276.2		1187.5	

* seed ± stone only

At the end of the feeding trial, fruit remains were collected, sorted to species and weighed and a description made of each fruit's condition. For each individual fruit within each species, an estimate was made of the relative percentage of pericarp which remained. Small fragments of (uneaten) seed and pericarp found on the cage floor were included in estimates of % fruit and seed remaining. Seeds were identified and counted.

Although assembled remains of each fruit species were individually weighed for each animal, this gave no indication of the type of damage, or the likelihood that an animal had actually eaten the fruit or seed. For example, an animal could have torn or stood on the fruit, due to stress during its captive condition. For analysis, the fruit and seed of each species were classed as untouched, damaged or eaten. This gave a more conservative estimate of whether fruit was of interest for eating. Fruits were classed as 'damaged' if they were whole with $\leq 5\%$ damage, or if $>75\%$ of the area of exocarp originally offered was retrieved after sorting the sample. Thus 'damaged' fruits included those where animals may have eaten the fleshy mesocarp from beneath, but left the exocarp uneaten, or where the fruit was broken apart in order to access the seed(s). Small fruits were classed as eaten if $\geq 25\%$ of the total pericarp area from all fruits was missing. Large fruits were classed as eaten if $>25\%$ fruit flesh was removed from at least one fruit.

Classification of seed condition depended on the species concerned. For *A. brachiandra*, *Millettia australis*, *C. australe*, *Macadamia* (i.e. large seeds) and *Cinnamomum camphora* (1 seed/fruit), seeds were classed as 'damaged' if they were whole with $\leq 5\%$ damage, and eaten, if a greater percentage was removed. In the case of *Macadamia*, the very hard endocarp could be gnawed without any damage to the endosperm within. The endocarp was never classed as eaten, despite some significant damage, as consumption of the woody tissue seemed unlikely, or unintentional. Due to the large number of seeds produced within the fleshy layer of *Ficus* spp., seeds were classed as eaten if some were obviously missing or damaged, and were only classed as damaged where only the fruit pericarp was eaten, leaving the central core of seeds $<25\%$ disturbed. For each berry species, the average number of seeds held in 10 fruits was determined, and this was used to calculate the expected number of seeds contained within the number of fruits offered. For *Citriobatus pauciflorus* (8 seeds per fruit) and *Cordyline rubra* (4 seeds/fruit), seeds were classed as eaten if more than two seeds were missing from the expected number of seeds held within the fruit. For *Cissus* sp., which may hold one or two seeds per fruit, the lower number (1 seed per fruit) was used. This gave a conservative estimate of seeds, thus ensuring that seeds were only classed as eaten if more than one was clearly missing. For multi-seeded berries, it was less clear whether seeds had been eaten, due to the variable number of seeds held within individual fruits. For *Solanum pseudocapsicoides*, *Pittosporum undulatum* and

S. mauritianum, seeds were classed as damaged if found with >75% of the expected number present. Seeds were classed as eaten if <75% of the number expected were present. In most cases, the distinction was very clear.

To check the actual quantity missing from each animal's cafeteria, the total diaspore remaining was weighed for each animal. This weight included moisture loss from the fruits due to evaporation. To correct for this, undamaged and largely undamaged fruits and seeds from the trial were used to estimate average moisture loss for each plant species. For damaged fruits, the original weight was corrected for the percentage of fruit and number of seeds remaining, and the moisture loss then calculated. The average moisture loss from undamaged and damaged fruits of each species was used to calculate estimated weight loss for each sample of fruit originally offered. These weights were summed, to give an overall estimated moisture loss from the rodent and *T. caninus* cafeterias. Corrected total weight of diaspore eaten by each animal was then calculated.

5.3.4 Comparison of *C. australe* seed damage and fauna at five sites

At each of the five sites, the types of fruit and seed damage were observed during 1989. To investigate the relationship between presence/absence of major seed predators and seed predation, a small mammal survey was conducted concurrently in the five remnants, in June 1989 and again in June 1990. Two 100 m traplines were placed in each remnant, with 11 ground traps at 10m intervals and 6 arboreal traps at 20 m intervals per transect. In 1990, large and small elliot traps were alternated at the ground stations; otherwise only small elliot traps were used. Trapping was carried out over two nights in 1989 and over four nights in 1990. Between 3-7 cage traps baited with apple (with a peanut and oat-baited small elliot placed inside each cage) were also placed at each site in September 1989. Larger mammals were also recorded from spotlight surveys and opportunistic sightings. Additionally, 10 cage traps were placed at Big Scrub F.R. in June 1990, concurrent with small mammal trapping. This provided a test of the correlation between seed predators identified in this study, and predation observable in the field.

5.4 RESULTS

5.4.1 Patterns of damage by insects

Seeds were damaged by insects in a range of ways.

(1) Some fresh firm seeds were found with an obvious broad hole or series of surface holes, consistent with damage by an insect with chewing mouthparts. One of the holes often

penetrated deeper into the centre of the seed (Figure 5.2). Lepidopteran larvae were found in a few of these seeds (Table 5.2). The Pyralidae and Gelechiidae/Oecophoridae were found in freshly eaten cavities in fresh seeds, and appear to be seed predators. Other insects (earwig (46); Coccinellidae larvae (Coleoptera, 54), adult *Steiidota variabile* (Nitidulidae, 22); Hemiptera (51)) were also found in firm, chewed seeds, but were regarded as subsequent invaders.

(2) Firm seeds were also found with a linear pattern of superficial chewing damage, often in the region of the hilum. Further investigation revealed that small bore holes within this surface damage could lead to a region of greater damage with softened tissue within the centre of the seed. This region is not visible from the exterior of the seed. This softened region often contained adult beetles and their larvae (*Paraphloeostiba gayndahensis*: Staphylinidae (23, 48)). Some seeds were found with a surface region of pitted black chewed tissue and fine bore holes (Figure 5.3). These probably also commenced with the linear surface damage described above.

(3) Seeds which had commenced germination were sometimes found with the root and surrounding cotyledon tissue blackened and soft (necrotic). The underlying tissue was soft and mushy, or dry and granular in appearance. One seed contained Dipteran larvae (Nematocera? 47, Syrphidae 52), and adult Ptiliid beetles (12). Another seed contained adult and larval *P. gayndahensis*, Syrphid larvae (52) and two adult Ptiliid beetles (20?).

(4) Seeds with evidence of decay from other means contained large numbers of Dipteran larvae, and adult and larval *P. gayndahensis*. These seeds had either previously been eaten by vertebrates, or had decayed due to damaged or necrotic tissue.

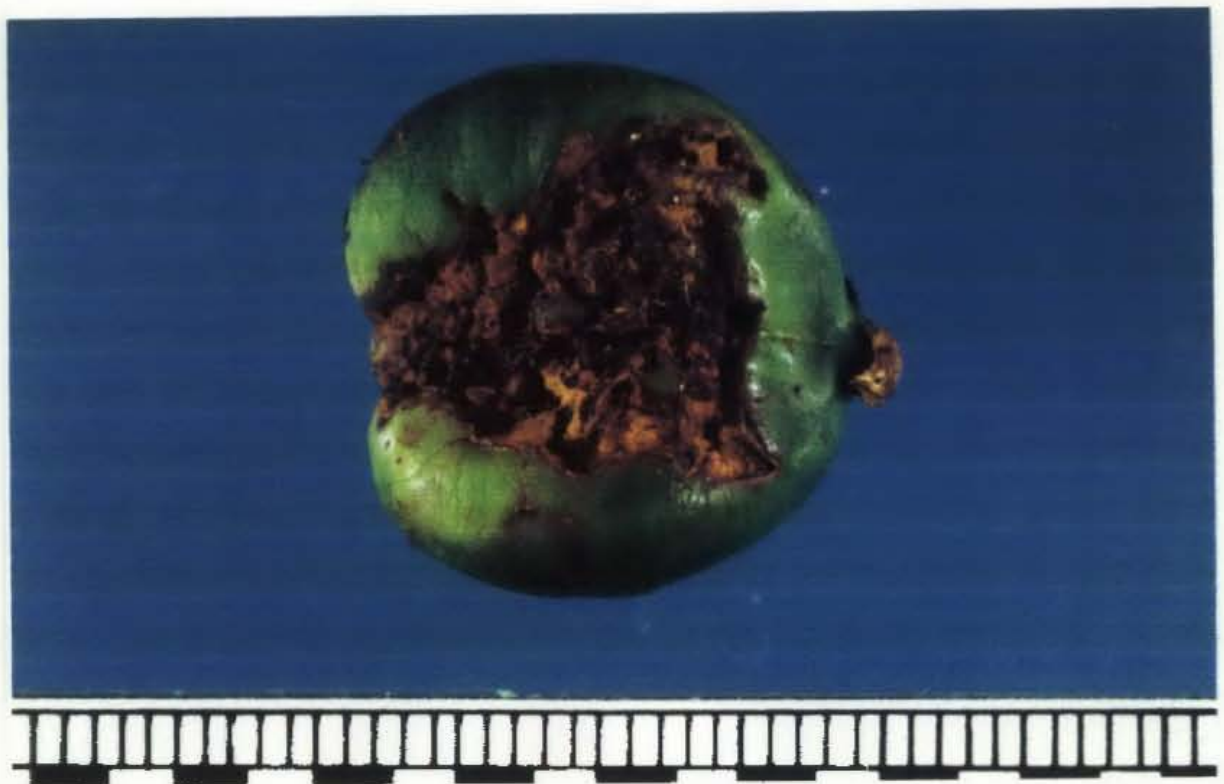
In addition to those described above, a range of other insects were found within pods, in seeds or on seedlings (Appendix 1). No bruchid beetles were found and none of the coleopteran species found within or on damaged seeds appear to be seed predators (J. Lawrence pers. comm.). Other invertebrates such as stratiomyiids and mites were found in seeds of a range of conditions, in particular within rotting, insect damaged seeds, and were also found within the pods, presumably eating the spongy mesocarp or its inhabitants. The majority of the insects are scavengers and fungivores (J. Lawrence pers. comm.), rather than seed predators.

Figure 5.2 Photograph of insect chew hole in seed.
(Fine gradations on scale = 2mm)



Photography: Media Resources Unit, University of New England

Figure 5.3 Photograph of pitted bore-hole region in seed (insect predation).



Photography: Media Resources Unit, University of New England

Table 5.2 Lepidopteran larvae* collected from damaged *C. australe* seeds and seedlings.

Spec. No.	Family	Site	Date	Seed description
1	Pyralidae	Wollongbar	28/12/89	eating outside of firm seed.
		Davis Scrub	19/2/92,20/7/94	in freshly-chewed seed.
2	Gelechiidae or Oecophoridae	Big Scrub F.R.	2/11/94	in freshly-chewed hole in firm seed.
3	Alucitidae	Victoria Park	19/9/94	in partly damaged seed.
4	Alucitidae	Big Scrub F.R.	Sept 1991,20/9/94	in damaged seed.
35	Noctuidae	Wollongbar	28/12/89	eating firm seed.
87	Geometridae	Davis Scrub	16/1/92	on seedling

*larvae identified by J.F. Donaldson, Department of Primary Industries (Dept. Entomology), Meiers Road, Indooroopilly, Queensland.

5.4.2 Mammal predation: Observation of patterns of eaten seed.

Two main patterns of seed consumption were observed. The first type formed multiple small scrapes in a horizontal plane across the top of the seed. Scrape marks were the width of two rodent incisors or a little wider, and in dry weather, the separate incisor marks were distinct. Scrape marks were random in their direction across the seed (Figure 5.4), but were sometimes formed in a radial pattern as the seed or animal rotated. Occasionally the indentation of the opposing set of incisors was also visible at the edge of the uneaten portion. No particular portion of the seed was eaten first. Freshly eaten seeds often had numerous small fragments (ca 4-8 mm diameter) lying beside the larger uneaten portion. Seed damage by this means spanned from <1% damage (incisor marks only, or one scrape) to only small fragments remaining (ca 2% remaining). Seeds were often found in the buttress of a tree, on a rock or log, or in the shelter of a large fallen log.

The second type of damage was incurred by a broader set of incisors. Usually, the opposing set of incisors were used to grip the seed, leaving a series of neat indents in the undersurface of the seed. The upper portion of the seed was eaten in a radial pattern. This indicated that the seed was held firm as the upper incisors were dragged across the seed, then the seed was rotated by hand before another scrape was made (Figure 5.5). If a large proportion of the seed was eaten, this resulted in a cavity being formed in the centre of the seed, forming a bowl or 'shell' shape. Seed damage by this means spanned from <1% damage (incisor marks

only, or one scrape) to a single small fragment or thin shell remaining (ca 5% remaining). Occasionally puncture marks were also evident in the uneaten portion. These were presumably formed by claws. Seeds were often found on the ground, on a rock, log or stump, or in the buttress of a tree. For both predators, seeds were sometimes found under a low-lying spray of Lawyer Cane *Calamus muelleri*.

5.4.3 Matching incisor marks on field seeds with skulls in laboratory.

Seeds with the first type of damage (above) were obviously eaten by a rodent. The broader tooth marks were made either by *T. caninus* or *Thylogale* spp. Tables 5.3 and 5.4 give the measurements taken from incisor marks in *C. australe* seeds, and skulls of *R. fuscipes*, *M. cervinipes*, *T. caninus*, *T. thetis* and *T. stigmatica*.

Whether the rodent teeth marks in seeds were due to *R. fuscipes* or *M. cervinipes* could not be distinguished. Although the width of upper incisors did differ significantly between skull species (t-test, $p < 0.01$; Table 5.3), for all measurements the ranges overlapped, and in any case were not consistent with marks in seeds (Table 5.3). However the size and pattern of damage distinguished rodents from those seed predators with broader teeth. On reasonably fresh seeds the separate rodent incisor marks could be distinguished by eye. On older seeds, the separation between individual incisors became indistinct, sometimes leaving marks similar in width and arrangement to those of single incisor indents formed by the predator with broad teeth. Inspection under a hand lens or microscope often clarified the separation of individual incisors, and the pattern of gouging also distinguished rodents from those of the broad-toothed predator. Rodent teeth marks were sometimes evident as scrapes along the seed testa (Figure 5.6) and sometimes fine scratch marks were evident on the seed coat (marks made by claws).

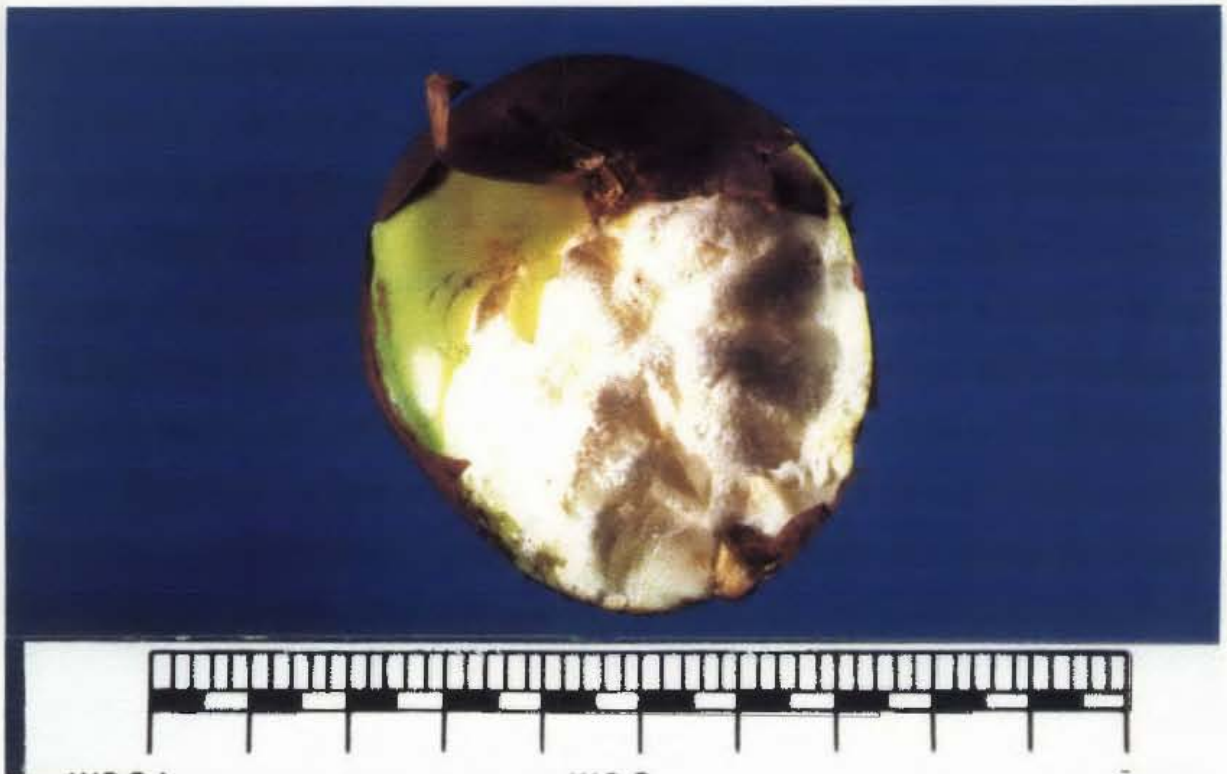
Of the seeds with broad-toothed damage, all but a few matched with *T. caninus*. The most reliable method of distinguishing *T. caninus* and *Thylogale* spp. bite marks in seeds was by visual comparison with patterns of teeth marks in plasticine (Figure 5.7). Most tooth measurements for the two *Thylogale* species were not significantly different (t-test, $p < 0.05$; Table 5.3) and subsequently, *T. caninus* teeth measurements were compared with *T. stigmatica*. Between teeth of *T. caninus* and *Thylogale* spp., some single-character measurements were significantly different (Table 5.3). However, the range of measurements often showed strong overlap, and in practice was not a reliable method of distinguishing species. Measurements of teeth did not generally compare well with marks in seeds. This was due to the resistance offered by the seed tissue, and the differing depth and angle of incision made by different animals and bites. For most measurements of seeds

Figure 5.4 *C. australe* seed eaten by a rodent.



Photography: Media Resources Unit, University of New England

Figure 5.5 *C. australe* seed eaten by *Trichosurus caninus*.



Photography: Media Resources Unit, University of New England

Figure 5.6 Marks made by a rodent scraping incisors across seed testa



Photography: Media Resources Unit, University of New England

bitten by *T. caninus*, the range of values was broader than those measured for teeth, indicating that *T. caninus* manipulated seeds in a range of ways, including firm, deep bites which tore the seed.

T. caninus upper incisor marks can be visually distinguished from those of *Thylogale* spp. (Figure 5.7). Aside from the distinctive patterns, species differed in ability to grip the seeds. In *Thylogale*, the upper incisors did not puncture the seeds deeply (indicating that they can only grasp the seeds). *T. caninus* bit seeds firmly. Upper incisors appeared to be used mainly for gripping the seed firmly, but this left a deeper impression. Some superficial bites showed clearly that both upper and lower teeth can be used for biting through the seed.

Probably because *T. caninus* lower incisors are used for gouging through the seed, there were fewer clear sets of lower incisor marks on the seeds examined. Lower incisor marks sometimes overlapped considerably, as if the teeth were re-positioned several times before proceeding through the seed. *Thylogale* lower incisors did not bite into the seed to the depth of the base of the cusp, i.e. marks made by incisors in seeds were smaller than

measurements of the base of the cusp. This indicates that seeds were only lightly grasped by the tips of the incisors, or that the seed offered too much resistance for a firm bite.

There is no clear evidence that *Thylogale* spp. eat *C. australe* seeds, but there is evidence that they will handle or move seeds. Two seeds collected in September 1991 from Big Scrub F.R. had teeth marks which clearly matched with plasticine imprints made by teeth of *Thylogale* spp. The seeds had <1% damage made by the scrape of teeth through the testa and cotyledon. Neither seed had been chewed. One seed was found under a tree at Big Scrub and had a small wet area on the upper surface. The seed was found during the afternoon, when all dew had dried and there had been no rain. The wet mark was apparently freshly formed by saliva, and indicates that *Thylogale* will handle seeds. The area of paint on the seed had been scraped by teeth. A fresh seed found at Johnston's Scrub was superficially scoured, and gouge marks matched with the upper and lower incisors of *Thylogale* spp.

Figure 5.7 Comparison between *Thylogale stigmatica*, *T. thetis* and *Trichosurus caninus* dentition and incisions made in plasticine.

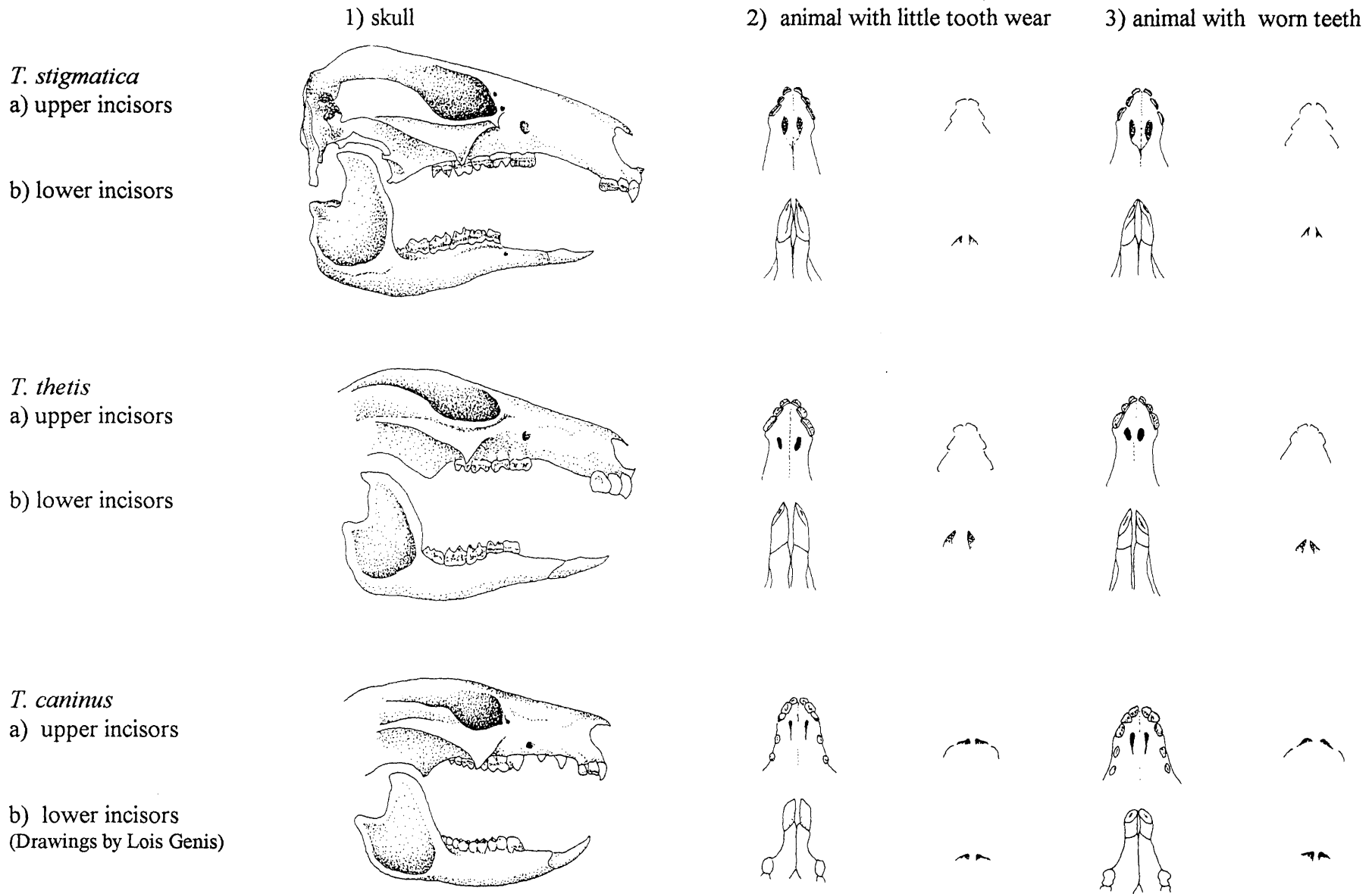


Table 5.3 Measurements of upper and lower incisors of *R. fuscipes* and *M. cervinipes*, and of rodent teeth marks in *C. australe* seeds.

	Skulls <i>R. fuscipes</i>		<i>M. cervinipes</i>		Seeds*	
	mean	range	mean	range	mean	range
<u>Lower incisors</u>						
Total width 2 teeth	2.83 ^a	2.17-3.25	2.56 ^a	2.5-2.67	2.03	1.35-3
Thickness (cut)	0.78 ^a	0.42-1.17	0.68 ^a	0.5-0.83	0.6	0.1-1.45
Width front teeth	1.14 ^a	0.92-1.33	0.87 ^b	0.75-1	1.06	0.65-1.85
Dist. b/w incisors	0.51 ^a	0.13-0.92	0.8 ^a	0.75-.83	0.002	0-0.01
Dist b/w peaks	1.33	-	1.25	1.17-1.33	1.31	0.8-1.9
<u>Upper incisors</u>						
Total width 2 teeth	2.7 ^a	2.5-2.83	2.23 ^b	1.83-2.58		
Thickness (cut)	1.16 ^a	0.75-1.5	1.22 ^a	1.08-1.33		
Width front teeth	1.32 ^a	1.17-1.5	1.1 ^b	0.83-1.33		
Dist. b/w incisors	0	-	0	-		
Dist b/w peaks	0.83 ^a	-	0.87 ^a	0.83-1		

*Rodent upper and lower incisor teeth marks were not distinguishable on seeds.

Table 5.4 Measurements of upper and lower incisors of *T. caninus* and *Thylogale* spp., and of teeth marks in *C. australe* seeds.

	Skulls			Seeds	
	<i>T. caninus</i>	<i>T. stigmatica</i>	<i>T. thetis</i>	<i>T. caninus</i>	<i>Thylogale</i>
	mean	mean	mean	mean	mean
<u>Lower incisors</u>					
Total width 2 teeth	7.13 ^a	7.18 ^a	8.06 ^a	6.85 ^d	3.61 ^e
Arc teeth	2.78 ^b	5.08 ^a	4.15 ^a	1.51 ^d	2.13 ^e
Cut teeth	1.75 ^a	1.89 ^a	1.9 ^a	1.36 ^d	2.18 ^e
Width front teeth	3.53 ^a	2.57 ^a	3.11 ^b	3.02 ^d	1.35 ^e
Dist. b/w incisors	1.58 ^a	1.61 ^a	0.92 ^a	0.99 ^d	0.98 ^d
Dist b/w peaks	2.68 ^a	0.15 ^a	1.24 ^b	3.01 ^d	1.73 ^e
<u>Upper incisors</u>					
Total width 4 teeth	9.94 ^b	7.69 ^a	8.13 ^a	8.87 ^d	8.7 ^d
Arc4 teeth	4.38 ^a	4.15 ^a	4.15 ^a	3.89 ^d	3.93 ^d
Total width 2 teeth	5.44 ^a	5.6 ^a	5.57 ^a	5.45 ^d	4.77 ^e
Arc front teeth	1.37 ^(a)	1.59 ^a	1.53 ^a	1.56 ^d	2.23 ^e
Cut front teeth	1.68 ^b	1.98 ^a	2.24 ^c	1.02 ^d	1.1 ^d
Width front teeth	2.3 ^b	2.9 ^a	3 ^a	2.38 ^d	4.08 ^d
Dist. b/w incisors	0.78 ^b	0 ^a	0.32 ^a	0.85 ^d	0.17 ^e
Dist b/w peaks	2.29 ^b	1.31 ^a	1.41 ^a	2.5 ^d	0.83 ^e

Species were compared for skull dimensions, and separately, for dimensions of teeth marks in seeds. For the comparisons above, means without superscripts in common are significantly different ($p < 0.05$, one-tailed t-test) between species. Skulls were not compared statistically with marks in seeds, due to the lack of correspondence within species.

5.4.4 Feeding trials

All animals in the trials (5.3.3) ate some fruit and seed. Table 5.5 gives the total weight of fruit and seed missing from each animal's cafeteria at the end of the trial. This weight includes moisture loss from the fruits due to evaporation. The final column in Table 5.5 gives the corrected amount eaten by each animal, as a percentage of body weight. There was a significant difference between animal species in quantity of food eaten (ANOVA, $F=6.5$, $df=3$, $p<0.001$; Figure 5.8), probably a result of different body weight and food requirements between genera, but all animals consumed $> 7\%$ of their body weight.

Most fruit species were at least superficially damaged by most animals (Table 5.6), probably because animals were captive. However, some fruits and seeds were consistently eaten: *T. caninus* devoured the ripe *F. macrophylla* and ate some fruit flesh of *A. brachyandra*, then moved to eating the fruit and seeds of *C. camphora*, *S. mauritianum*, and the seeds of *Macadamia* and *C. australe*. Early in the trial, all *R. fuscipes* had eaten the ripe *F. watkinsiana*, and at least investigated the *C. australe* seeds. *R. fuscipes* consistently ate the seeds of *Cordyline* and *C. australe*, and the fruit and seeds of *S. mauritianum* and *C. camphora*. Many small fragments of *C. australe* seed were found during sorting, but this is consistent with observations in the field where a lot of the chewed seed is also dropped. All individuals gnawed *Macadamia* endocarps and two successfully ate the seed. *Melomys* individuals consistently ate soft fruits, in particular *Ficus spp.*, *Cordyline*, *C. camphora*, and *A. brachyandra*, and the seeds of *Ficus spp.*, *S. pseudocapsicoides*, *Cordyline*, *P. undulatum*, *C. camphora* and *S. mauritianum*. One individual gnawed through a cracked *Macadamia* shell and ate the seed. Late in the feeding trial, the juvenile individual significantly damaged a *C. australe* seed (seed 80% remaining). *R. rattus* ate the ripe fruit of *F. watkinsiana*, seeds of *S. mauritianum*, and fruit and seeds of *Cordyline* and *C. camphora*. They damaged several other species, including *C. australe* seeds, but did not eat the latter.

For a few diaspore species, the criteria used to classify damage were necessarily conservative, and thus may have excluded some diaspore consumption. For example, *Citriobatus pauciflorus* seeds were obviously eaten by one *R. fuscipes*, as only two damaged seeds remained. However, for the other two animals the number of seeds remaining was within the expected range, and it was unclear whether some seeds had been removed. Despite the definitional problems, it was clear that all animals ate something other than *C. australe*, and thus did not eat *C. australe* seed out of complete lack of alternative foods. The two species which consistently ate, rather than damaged *C. australe*

seeds were *R. fuscipes* and *T. caninus* (Table 5.7). Four out of five *M. cervinipes* damaged at least one *C. australe* seed, but only one individual damaged a seed more than 5%.

Table 5.5 Weight of diaspore consumed by animals during feeding trial (as an indication of sufficient food sources available, alternative to *C. australe* seeds).

Species	Animal No.	Sex	Animal weight at catch (g)	Weight missing* from cafeteria (g)	% of body wt.	Corrected % body wt.
<i>M. cervinipes</i>	1	M	81	45.09	55.6	38.0
	2	juv	58	37.64	64.9	40.2
	6	F	63	39.6	62.9	40.1
	7	F	64	46.2	72.2	49.8
	11	F	92	57.65	62.7	47.1
<i>R. fuscipes</i>	3	M	166	45.02	27.1	18.5
	4	M	126	40.43	32.1	20.7
	8	M	155	53.3	34.4	25.2
	9	M	143	54.04	37.8	27.8
	10	M	158	72.77	46.1	37.0
<i>R. rattus</i>	5	F	67	27.45	41.0	19.6
	12	F	111	48.29	43.5	30.6
<i>T. caninus</i>	1	F	2860	350.49	12.3	10.1
	2	M	3200	311.17	9.7	7.8

* includes moisture loss from foods during trial (ca 24 hours), estimated as a maximum of 14.31g from rat cafeteria, and 62.05 g from bobuck cafeteria, based on average % moisture loss calculated for each fruit species (including damaged and not), then summed.

Figure 5.8 Relationship between body weight of animals and diaspore weight eaten during feeding trial

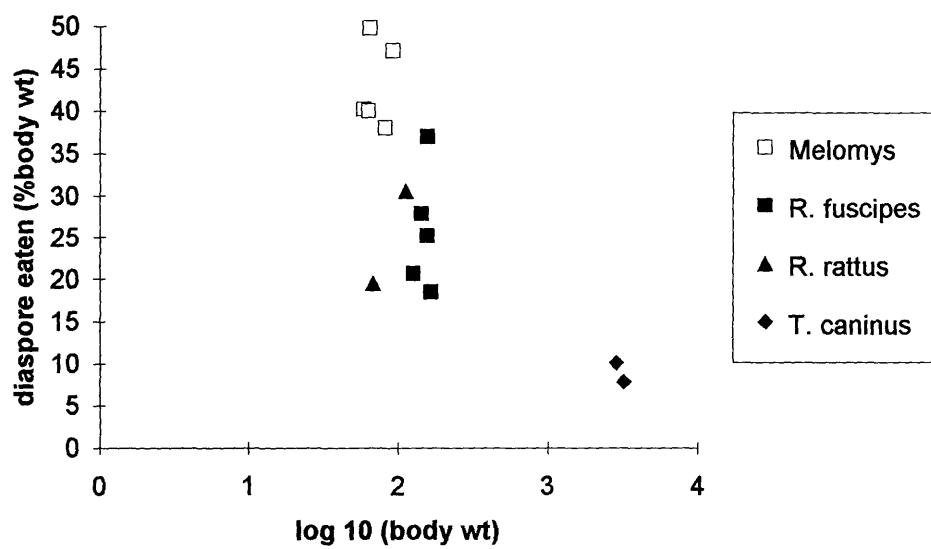


Table 5.6 Number of animals which damaged or ate fruit during the feeding trial, in which a cafeteria of fruit species was offered to captive wild animals.
(F=fleshy outer of fruit, S=seed, E=endocarp, dam=damaged. Animals unaccounted for in the following numbers did not damage fruit/seed).

Species		<i>Melomys</i>		<i>R. fuscipes</i>		<i>R. rattus</i>		<i>T. caninus</i>	
		(5)	(5)	(5)	(5)	(2)	(2)	(2)	(2)
Diaspore condition:		dam.	eaten	dam.	eaten	dam.	eaten	dam.	eaten
<i>Ficus watkinsiana</i> (ripe)	F	0	5	0	5	0	2	0	2
	S	-	5	-	5	-	2	-	2
<i>F. watkinsiana</i> (green)	F	2	2	2	0	1	0	1	0
	S	0	1	0	0	0	0	0	0
<i>Ficus superba</i> (green)	F	2	3	4	1	1	1	0	0
	S	1	2	0	1	0	0	0	0
<i>Acmena brachiandra</i>	F	1	4	4	0	2	0	2	0
	S	0	2	0	0	0	0	2	0
<i>Macadamia</i> (uncracked)	E	4	-	5	-	2	-	2	-
	S	0	0	0	2	0	0	0	0
<i>Macadamia</i> (cracked)	E	4	-	4	-	2	-	2	-
	S	-	1	-	2	-	1	-	2
<i>Cissus</i> sp.	F	4	1	3	2	1	1	1	1
	S	0	5	1	1	0	1	0	0
* <i>Solanum pseudocapsicoides</i>	F	3	0	1	1	1	0	2	0
	S	0	3	0	1	0	0	0	2
<i>Solanum mauritianum</i>	F	3	2	3	2	1	1	0	2
	S	1	4	0	3	0	2	0	2
* <i>Citriobatus pauciflorus</i>	F	0	2	2	1	0	0	0	0
	S	0	2	1	1	0	0	0	0
<i>Millettia australis</i>	S	1	0	0	0	0	0	0	0
<i>Cordyline rubra</i>	F	0	5	4	1	0	2	2	0
	S	0	5	1	4	0	2	0	0
<i>Pittosporum undulatum</i>	F	2	3	4	0	1	0	1	0
	S	0	4	2	0	0	0	0	0
<i>Cinnamomum camphora</i>	F	0	5	0	5	0	2	0	2
	S	0	5	0	5	0	2	0	2
<hr/>									
<i>C. australe</i> pod (<i>T. caninus</i>)	F	-	-	-	-	-	-	2	0
<i>C. australe</i> (fresh, Johnst)	S	3	1	0	5	2	0	0	1
<i>C. australe</i> (fresh, Davis)	S	2	0	1	3	2	0	1	1
<i>C. australe</i> (old, Davis)	S	1	0	1	4	1	0	0	2

*Due to shortage of fruits, these species were only offered to two or three individuals of each rodent species.

Table 5.7 Response of individual captive wild animals to *C. australe* seed offered amongst a cafeteria of rainforest fruit.

Animal species & No.	Untouched	Damaged		Eaten	
		No. seeds	% seed remaining	No. seeds	% seed remaining
<i>Melomys cervinipes</i> (5)					
1		3	(98,99,93)		
2	2			1	(82)
6	3				
7	1	2	(99.6,98.2)		
11	2	1	(98.7)		
Total	8	6		1	
<i>Rattus fuscipes</i> (5)					
3				3	(91,63,88)
4		1	(98.6)	2	(66, 84)
8	1			2	(91, 11)
9				3	(45, 53, 19)
10		1	(99.2)	2	(37, 8)
Total	1	2		12	
<i>R. rattus</i> (2)					
5	1	2	(99.9, 100)		
12		3	(97.6, 100, 99.4)		
Total	1	5		0	
<i>Trichosurus caninus</i> (2)					
1	3	1	(99.5)	2	(10, 6)
2	3			3	(75, 73, 93)
Total	6	1		5	

Comparison between species for total number of seeds in each damage category gave $\chi^2 = 29.5$, $df=6$, $P < 0.001$.

5.4.5 Comparison of types of *C. australe* seed damage at five sites, with fauna survey

Table 5.8 presents the results of fauna surveys at the five sites. All small mammal species which are facultatively or obligately present in rainforest (*R. fuscipes*, *M. cervinipes*, *A. stuartii* and *T. caninus*, see Table 3.7) were found at Big Scrub F.R. and Boomerang Falls. At Johnston's Scrub, both the native *R. fuscipes* and introduced *R. rattus* were caught, and one *T. caninus* was detected. *Rattus fuscipes* were absent from Wollongbar and Davis Scrub, but introduced rodents were caught at these sites. Two species of possum were seen at Wollongbar (Table 5.8). One *T. caninus* was seen on the edge of Davis Scrub in 1990, but none in the remnant interior. The relative abundances of species differed between sites and years, but only presence/absence is considered here, due to the low intensity of trapping. However, the trapping results are consistent with more intensive trapping conducted at Davis and Johnston's Scrub in 1991 (N. Campbell unpublished data, see Appendix 3) and at Big Scrub in 1989 (G. Watts unpublished data, see Appendix 3).

The types of fruit damage and seed predation (Table 5.9) which occurred under study trees at Big Scrub F.R., Boomerang Falls and Johnston's Scrub were correlated with the presence of the seed predators (*R. fuscipes* and *T. caninus*) at these sites. At Wollongbar and Davis Scrub seed predators were absent or occurred sporadically, and levels of seed predation were correspondingly low.

Fresh, firm seeds of *C. australe* with broad-toothed damage were found at all sites, but at Davis Scrub, only a few seeds were found damaged in this manner, and they were at two trees at the edge of the remnant. This corresponded with trapping and spotlighting surveys which indicated that *T. caninus* was not resident in the study area at Davis Scrub, but was observed in a nearby hollow tree stump at the edge of the remnant. Fresh seeds with rodent damage were only found at the three largest sites. This corresponded with the occurrence of *R. fuscipes* at these sites. Seeds damaged by rodents at Wollongbar and Davis Scrub were apparently decayed prior to predation. This suggested that these seeds were eaten by a different species which was unable to deal with the toxins in fresh seeds. *Rattus rattus* was trapped at these two sites.

It is possible that *Thylogale* will occasionally eat a portion of decayed seed. Most of the (few) broad-toothed marks seen on seeds within the core of Davis Scrub remnant were in partly decayed seeds. The occasional decayed seed was also eaten by a broad-toothed animal at Big Scrub. The pattern of gouging did not leave a bowl or shell-shaped cavity in the seed. Rather, the eaten surface was relatively flat after the initial deep cut into the seed

Table 5.8 Small mammal live trapping survey for 5 remnants of the *C. australe* - *D. muelleri* association within the Big Scrub. Total number trapped or sighted during spotlighting, excluding recaptures.

Trapping was conducted at the 5 sites concurrently. Trapping effort per site was 68 trapnights in 1989, and 136 trapnights in 1990 (2 x 100 m transects, containing 11 ground and 6 arboreal eliott traps per transect, over 2 nights in 1989 and 4 nights in 1990).

		BS 148ha	Boom 62ha	Johnst 21ha	Woll 2ha	Davis 11ha
<i>Antechinus stuartii</i>	1989	16	4	0	0	0
	1990	32	1	0	0	0
<i>Isoodon macrourus</i>	1989	1*	0	0	1	0
	1990	2*	0	1*	2	0
<i>Pseudocheirus peregrinus</i>	1989	1*	-	-	2*	-
	1990	0	0	0	1*	0
<i>Trichosurus caninus</i>	1989	-	-	-	1*	-
	1990	3(+4 [^])*	5*	1*	1	1*
<i>Melomys cervinipes</i>	1989	4	1	0	0	0
	1990	6	1	0	0	0
<i>Rattus fuscipes</i>	1989	3	3	6	0	0
	1990	13	21	2	0	0
<i>Rattus rattus</i>	1989	0	0	1	1	1
	1990	0	0	0	2	0 (1 [^])
<i>Mus musculus</i>	1989	0	0	0	0	0
	1990	0	0	0	0	2

* spotlighting survey

- not surveyed

[^] opportunistic sighting outside transect

(although the gouges themselves were scalloped, or drain-shaped). In one seed, part of the seed was obviously gouged by parallel teeth and the other part was relatively flat, without evidence of gouging. The gouge appears to have been formed by lower incisors, and the flat area appears to have been cut by upper incisors, the alteration of shape caused by the softer nature of the decaying seed. However, although two faecal pellets matching those

from *Thylogale* spp. were found near the tree, it was concluded that the seed predation at Davis Scrub was caused by *T. caninus*, but the softer seed allowed a shallower seed predation pattern.

Pods of *C. australe* were frequently found at Big Scrub F.R. with the spongy mesocarp scraped or scratched away. Here, pods which I had collected and opened for other experiments were frequently disturbed overnight, and the mesocarp eaten. The marks indicated that the animal had broad teeth or claws (Figure 5.9). Pods with the mesocarp scratched or gnawed away only occurred at the two sites at which *Thylogale* are known to occur, that is Big Scrub, where *Thylogale* are abundant, and sometimes at Davis Scrub, where only one individual is known to occur (Table 5.9).

C. australe pods were also found with the ends chewed away, and with scratch and claw marks on the woody epicarp (Figure 5.10). These were seen at several sites (Table 5.9). This animal had teeth and claws strong enough to force pods open to obtain seeds. *T. caninus* appears most likely to do this.

Table 5.9 Presence of potential *C. australe* seed predators at five sites and the occurrence of seed predation and pod damage at these sites in 1989.

	BS 148ha	Boom 62ha	Johnst 21ha	Woll 2ha	Davis 11ha
Seed predation- broad tooth	+	+	+	+	(+)*
- rodent	+	+	+	(+)*	(+)*
Pod exterior scratched or chewed	+	+	(+)	-	-
Spongy mesocarp scratched	+	-	-	-	+
<i>Trichosurus caninus</i>	+	+	+	+	(+)
<i>Thylogale</i> spp.	+	-	?	-	+
<i>Rattus fuscipes</i>	+	+	+	-	-
# <i>R. rattus</i>	-	-	+	+	+
<i>Melomys cervinipes</i>	+	+	-	-	-

See Table 5.8 for results of small mammal trapping and spotlighting survey in each site in June 1989 and 1990.

- () minor occurrence,
- * seeds usually decayed prior to predation,
- # introduced species,
- ? species presence unknown.

Figure 5.9 Pod of *C. australe* showing spongy mesocarp which has been gnawed or scratched



Photography: Media Resources Unit, University of New England

Figure 5.10 A chewed pod with scratch marks on the woody outer



5.5 DISCUSSION

5.5.1 Predators of *C. australe* seed and fruit

Several species of dipteran larvae were found on freshly chewed seeds, and appear to be seed predators. Legume seeds are often eaten by bruchid beetles (Janzen), however none of the beetle larvae collected in *C. australe* seeds and pods were found in firm freshly chewed seeds, nor are they known to eat seeds (J. Lawrence pers. comm.). Insect damage to seeds was far exceeded by that of mammals (Chapter 6).

The mammalian predators of *C. australe* seeds identified in this study were *T. caninus* and *R. fuscipes*. This is based on the feeding trial, matching teeth marks with seeds and the correspondence of predation patterns found in the field with presence/absence of these predators at the sites. Whether *M. cervinipes* eat the seeds is not certain. Patterns of rodent damage in seeds could not be distinguished between species, and melomys occur at the two largest sites where rodent damaged seeds were also found. However, they are not known to eat large quantities of seed (section 3.3.5), and the results of the feeding trial indicate that only naive juveniles will do more than investigate the seed. Although inconclusive, it seems unlikely that *Thylogale* spp. eat the seeds. Only three seeds were found with clear teeth marks attributable to these animals, and these seeds were barely damaged. If *C. australe* seeds formed a common part of *Thylogale's* diet, it should have been more evident within Davis Scrub. The patterns of damage also indicated that the alignment of incisors was not suitable for gnawing hard seeds. In any case, it is clear that they are not major predators of *C. australe*.

The presence of *Thylogale* teeth marks on seeds, but no clear chewing marks, suggests that they may move seeds in order to access and eat the mesocarp within the pods. This conclusion is supported by the observation that pods with the mesocarp scratched or gnawed away occurred only at the two sites at which *Thylogale* are known to occur, that is Big Scrub, where *Thylogale* are abundant, and sometimes at Davis Scrub (Table 5.9). Whether the spongy mesocarp is also eaten by *T. caninus* is not known. Given that *T. caninus* eats bark, lichen and other plant tissue (How 1983), it is possible that they would also find the sweet-smelling mesocarp attractive. However, if this were the case, pods with the mesocarp removed should have been more evident at other sites. The pods which were scratched and chewed were apparently forced open by *T. caninus*, and the seeds subsequently removed.

The relative proportions of each food eaten during the feeding trial are probably not representative of proportions eaten in the wild. For example, the response of wild *Rattus norvegicus* to novel foods is to sample a small quantity, but this may be no indication of future food preferences (Barnett 1956). Also, laboratory feeding experiments rarely offer the animal its full choice of diet, and the proportions of *C. australe* seeds eaten may depend on the other foods available: Herbivorous mammals may be less able to detoxify foods containing plant secondary metabolites than insects, and may minimise any adverse or toxic effects by mixing plant foods (Freeland 1991). However, the feeding trial used wild animals captured from the same locations as the foods offered, and animals should have been familiar with the fruits and seeds offered in the feeding trial. In this respect, those foods classed as eaten can be assumed to be a part of the diet of the species concerned.

Any animal which eats *C. australe* must either wait for the alkaloid to leach out of the seed, be able to detoxify it, or eat small quantities only. *R. fuscipes* is known to eat seeds with high levels of toxins (Ballardie & Whelan 1986). There is some evidence that *T. caninus* is able eat food with a high content of secondary compounds (van Dyck 1979), as does its congener *T. vulpecula* (Freeland & Winter 1975; Mead *et al.* 1979 in Hume 1982; Kerle 1985, Chippendale & Murray 1963).

5.5.2 Subtropical rainforest mammals as seed predators

R. fuscipes has been noted previously as a seed predator in rainforest (Freeland 1972) and in sclerophyll vegetation (Watts 1977, Cheal 1978). In only one other case has it been shown to eat large seeds (*Macrozamia communis*, Ballardie & Whelan 1986). *R. fuscipes* appears very adaptable in its diet selection, and it is likely that it eats other large-seeded species in habitats where other food sources are less available. For some plant species, it may have a significant effect on seed survival.

There is no information on the diet of *T. caninus* in rainforest. However, several factors suggest that it will eat other rainforest seeds, including large-seeded species. These factors are: 1) its dentition is suitable for gnawing seeds, and it has strong claws suitable for handling large fruits; 2) the diet of related species of possum includes nuts and nut-like fruits (section 3.3.5) and *T. caninus* may find nut-like fruits attractive (including *C. australe*); 3) *T. vulpecula* eats seeds in rainforest (Procter-Gray 1984) and other habitats (Fitzgerald 1984, Evans 1986, 1992); 4) in New Zealand, the introduced *T. vulpecula* eats fruit and seeds from several genera which are also found in rainforests of Australia (Appendix 5). New Zealand forests and Australian rainforest flora have a common Gondwanan origin (Adam 1992), and it would be interesting to investigate whether the

species which have become food for *T. vulpecula* in New Zealand, have congeners as food for *T. caninus* in Australian subtropical rainforest.

In Section 3.3.6, it was noted that *Thylogale* spp. have procumbent lower incisors which are pointed and inserted at an acute angle to each other. The angle of the lower incisors suggests a capacity for spearing, clipping and plucking foods, rather than gnawing. The results of this study indicate that this is indeed the case, and *Thylogale* are unlikely to eat *C. australe* seeds and other hard seeds, although they do eat softer fruit parts (Johnson 1983a). Both *M. cervinipes* and *R. rattus* ate fruit and seeds from several fleshy-fruited species offered in the feeding trial. This is consistent with observations of diet in other habitats (Watts & Aslin 1981), and indicates that both these species will eat small-seeded species in rainforest.